

The Recognition and Evaluation of Homoplasy in Primate and Human Evolution

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ABSTRACT Homoplasy has been a prominent issue in primate systematics and phylogeny for as long as people have been studying human evolution. In the past, homoplasy, in the form of parallel evolution, was often considered the dominant theme in primate evolution. Today, it receives blame for difficulties in phylogenetic analysis, but is essential in the study of adaptation. This paper reviews the history of study of homoplasy, methods of defining homoplasy, and methodological and biological factors that generate homoplasy. A post hoc definition of homology and homoplasy, based on patterns of character distributions and their congruence or incongruence on a cladogram, is the most consistent method of recognizing these phenomena. Defined this way, homology and homoplasy are mutually exclusive. However, when different levels of analysis are examined, it is seen that homoplasy at one level, such as adult phenotype, often exists simultaneously with homology at a different level, such as developmental process. Thus, in some cases, patterns of homoplasy may point to underlying similarities that reflect the shared heritage of a particular clade. This is an old concept that is being renewed on the strength of recent trends in developmental biology. Factors that influence homoplasy include character definition and a host of biological factors, such as developmental constraints, allometry, and adaptation. These interact with one another to provide explanations of homoplastic patterns. Because of the repetition of events, explanations of homoplastic features are often more reliable than those for homologous features, and serve as effective tests for hypotheses of evolutionary process. In some cases, particular explanations of homoplasy lead to generalizations about the likelihood of homoplasy in a type of structure. The structure may be adaptive or highly epigenetic, or it may belong to an anatomical system considered to be more prone to homoplasy than others. However, our review shows that these generalizations are usually based on theory, and contradictory expectations can be developed under different theoretical models. More rigorous empirical studies are necessary to discover what, if any, generalizations can be made about the likelihood of homoplasy in different types of characters. *Yrbk Phys Anthropol* 42:189-232, 1999. © 1999 Wiley-Liss, Inc.

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GLOSSARY

Adaptation: A trait is an adaptation for a particular function if it enhances the performance of that function and has been selected to perform that function.

Analogy: When different structures have a similar function in different organisms. This is similar to convergence, but with an explicit reference to function.

Character: A unit of information (i.e., a feature, trait, or structure) regarding an organism. A character state is one expression of a character.

Constraint or potential: A bias on the production of variant phenotypes or a limitation on phenotypic variability caused by developmental or genetic systems, or functional integration. This definition is adapted from Maynard-Smith et al. (1985), speaking of developmental constraints. Schlichting and Pigliucci (1998), among others, have noted that nongenetic constraints typically operate through natural selection; in that disruption of the development program or functional complex is selected against.

Convergence: Similarity in distantly related organisms. Convergence is sometimes distinguished from parallelism by lacking "detailed" similarity. It can also be defined as the separate evolution of functionally similar structures from different ancestral morphologies. Some authors use "convergence" as essentially a synonym for all homoplasy that is not reversal.

Homology: Similarity between two or more taxa that is inherited from their last common ancestor. Sometimes referred to as "true" similarity.

Homoplasy: Similarity between two or more taxa that is not inherited from their last common ancestor. Sometimes referred to as "false" similarity, parallelism, convergence, or reversal. Homoplasy can also be viewed as all similarity that is potentially misleading with regard to phylogeny.

Parallelism: The separate evolution of similarity in closely related organisms that occurs because of characteristics shared by those organisms, usually the genetic or developmental basis of the similarity. It can also be defined as the separate evolution of the same

descendant feature from the same precursor feature. Some authors use “parallelism” as essentially a synonym for all homoplasy that is not reversal.

Reversal: The occurrence of a character state in a descendant that is identical to a character state in a distant ancestor, but different from that in the immediate ancestor. Reversal can simply be the loss of a feature, in which case the descendant and precursor character states are “absence,” or the recurrence of a character state that was previously lost or modified.

Similarity: A character shared among taxa, organisms, or parts of the same organism. It may arise by shared or different pathways. Similarity varies from profound to superficial depending on the goals of the researcher.

INTRODUCTION

Homoplasy is most simply described as any similarity shared by two or more taxa that is not inherited from their last common ancestor (Fig. 1). The study of homoplasy, including parallelism, convergence, and reversal, has a long history in the study of primate and human evolution. Indeed, for much of this century the order Primates was defined by a series of parallel trends rather than homologous derived features. More recently, with the development and widespread use of quantitative computerized methods of phylogenetic systematics, the expression of homoplasy has been formalized and quantified as an important evolutionary phenomenon in need of further explanation.

Instances of homoplasy can be identified as methodological problems of analysis or as biologically meaningful events. As methodological error, homoplasy most often occurs because of poor *a priori* determination of homology. As a biologically meaningful phenomenon, homoplasy occurs when structurally identical characters evolve separately. Further analysis is necessary to reveal the extent to which this reflects parallel adaptation or some kind of constraint — developmental, genetic, structural, functional, or otherwise. Hypotheses of adaptation link morphology to the environment, and evidence of constraint may indicate an underlying similarity that characterizes the clade at a level other than adult phenotype.

In this review, we adopt the stance that both methodological and biological factors play important roles in generating observed patterns of homoplasy. We focus somewhat more on biological factors, as these are likely

to lead to productive research areas. Most of our discussion is directed toward morphological and behavioral data, which mainly reflects our areas of expertise. We (1) briefly review the history of homoplasy in general and with specific reference to primate and human evolution; (2) discuss alternative definitions of homoplasy with respect to homology and in the context of phylogenetic analysis; (3) address methodological and biological causes of homoplasy; (4) review prominent examples of homoplasy in primate and human evolution; and (5) conclude by outlining important areas of research on homoplasy that need to be pursued in the future. Throughout this discussion, the central theme is that patterns of homoplasy are informative about the evolutionary process.

We do not intend to use evidence of frequent homoplasy as a platform for criticizing the practice of phylogenetic systematics, as is sometimes done, or offer alternatives to cladistic methodology in the study of primate relationships. Indeed, cladistic methodology has largely encouraged the study of homoplasy by making its presence explicit.

A CENTURY AND A HALF OF HOMOPLASY

The term “homoplasy” was coined by the British comparative anatomist, Ray Lankester (1870, p. 39) who described it as correspondence in form that results “when identical or nearly similar forces, or environments, act on . . . parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic [homologous]”. Thus the term was introduced as a fairly specific kind of homoplasy, essentially parallelism, wherein

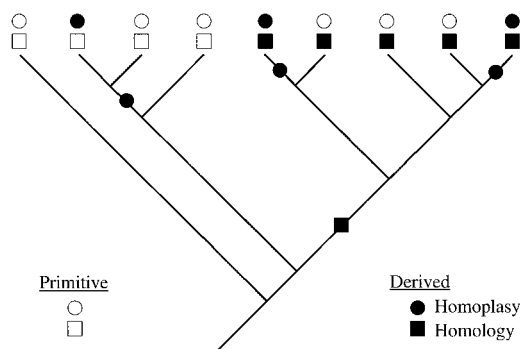


Fig. 1. Simplified cladogram to illustrate *pattern* definitions of homology and homoplasy. Characters "circle" and "square" both have two character states, empty and filled. The filled square is homologous across the taxa in which it is present, because the group defined by this trait is congruent with the phylogenetic tree, i.e., the common ancestor is reconstructed to have possessed the same character state. The filled circle is homoplastic, as the derived state supports a group that is incongruent with the phylogenetic tree, and the character state is not present in their last common ancestor.

features in two taxa are the same despite separate paths of evolution.

The phenomenon of homoplasy was well known to earlier comparative anatomists such as Owen, whose definition of analogy (Owen, 1843) overlaps with concepts of homoplasy and convergence, and Darwin (e.g., 1859). Panchen (1994) argued that the original explicit distinction between homology and homoplasy was made by MacLeay (1821) in reference to affinity and analogy, respectively. Even after the word "homoplasy" became available, more specific terms such as parallelism (or parallel evolution) and convergence were often preferred to describe homoplasy.

Terminology aside, instances of homoplasy impressed comparative anatomists and paleontologists during the late 19th and early 20th centuries. Observations of parallel evolution or convergence featured prominently in descriptions of the *pattern* of evolution as well as attempts to identify the evolutionary *processes* responsible for the diversity of life. This was true of the study of primates as well as other organisms. Virtually all scenarios of primate evolution from the early part of this century, and the phylogenies associated with them, involved extensive parallel evolution among the lineages lead-

ing to living primates (see Fleagle and Jungers, 1982; Cartmill, 1982a). For example, most researchers considered anthropoid features to have evolved in parallel in Old World and New World monkeys, as well as in tarsiers and anthropoids. With the notable exceptions of Sir Arthur Keith (1915, 1934) and W.K. Gregory (1934, 1951), most authorities felt that many similarities among different lineages of apes as well as the features shared by apes and humans were the result of parallel evolution (Fig. 2).

This seeming obsession with parallelism was largely the result of a widespread refusal to accept any evolutionary scenario that involved evolutionary reversal — the evolution of a species with a primitive state for a feature from an ancestor with a derived state for that feature. Thus, the presence of (specialized or derived) long fingers or short thumbs in living apes and the absence of these features in humans meant that humans branched off from the anthropoid lineage before the other apes, or at the same time, regardless of how many other features they shared in common. Because both reversal and parallelism constitute homoplasy, the tendency to favor parallel evolution and minimize reversal in developing phylogenetic schemes represented a preference for a certain kind of homoplasy. Parallel evolution was preferred because it fit well with teleological or adaptive concepts of progress in evolution. Drawing their inspiration from other paleontologists and biologists, most primatologists embraced some form of orthogenesis, or directed evolution, as a major process determining the pathway of primate and human evolution.

Most of the work on orthogenesis described nonadaptive trends (see review by Bowler, 1986). Some researchers, such as Berg (1926), were explicit in rejecting natu-

Fig. 2. Two phylogenies illustrating views of parallel evolution in primates from the first half of the century: **a:** Smith (1924); **b:** Le Gros Clark (1959). Smith's phylogeny implies parallelism because the trunk remained generalized while similarities among several branches evolved independently and in parallel from this trunk. Le Gros Clark drew extremely long lineages leading up to various modern primates, in this case hominoids. Again, the changes along these lines were seen largely to follow evolutionary trends of parallelism beginning with relatively generalized taxa.

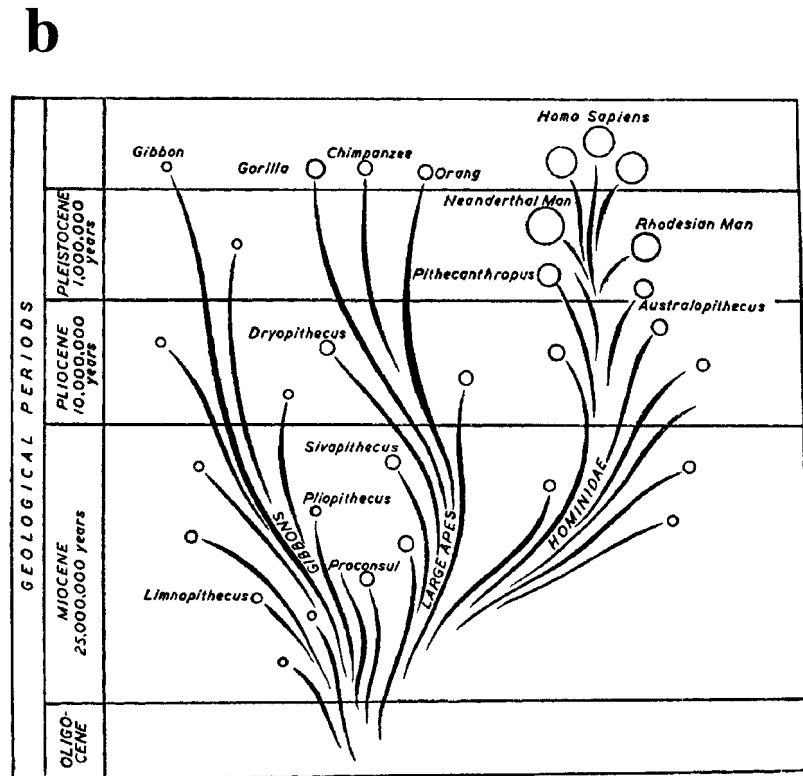
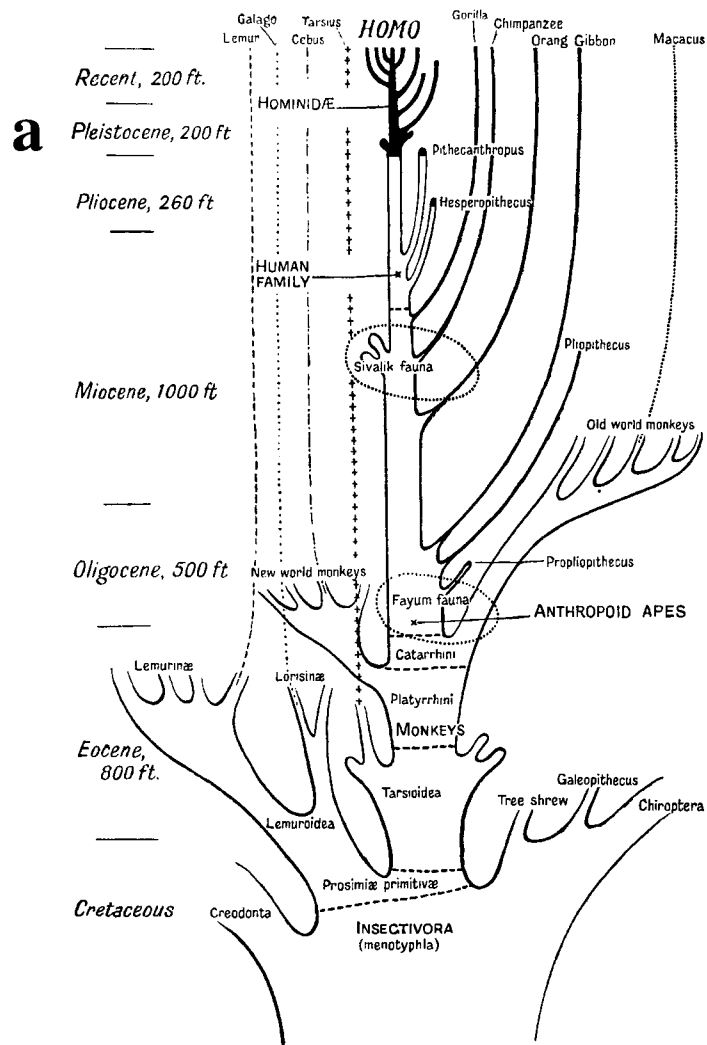


Fig. 2.

ral selection as a major influence on any macroevolutionary patterns. Other views of orthogenesis were more conservative and quite similar to modern day ideas of constraint (Grehan and Ainsworth, 1985; Jacobs et al., 1995; Shubin et al., 1997). Eimer (1890, 1898, cited in Grehan and Ainsworth, 1985) stressed that orthogenesis arose from physical and chemical processes and material composition of the body, which is a way of expressing restrictions on the evolution of morphology. In general, homoplasy as orthogenesis was used as a guide to phylogenetic relationships but not to adaptation, because the basis for homoplasy was intrinsic properties of organisms rather than natural selection. The opposite approach is usually taken today, although some workers, such as Groves (1989), still defend a law-like quality of parallel evolution that does not reflect primarily the action of natural selection, and many caution against inferring adaptation too readily from homoplastic events (Wake, 1991, and see below).

Although anthropologists incorporated some principles of orthogenesis into their understanding of phylogeny, they usually ascribed the "direction" of evolution to adaptive trends. This was due in large part to their desire to portray humans as the culmination of primate trends. As Fleagle and Jungers (1982, p. 193) describe this phase of research in primate evolution, "arguments over phylogeny were arguments over the functional pathways that led to human structure."

The combination of functional and adaptive arguments with phylogenetic interpretations was never more evident than in the work of W.E. Le Gros Clark, whose views dominated the study of primate and human evolution during the first three-quarters of this century. Le Gros Clark (1934, 1959) outlined a definition of primates that relied to a large degree on parallel evolution. Early primates (then considered to include plesiadapiforms as well as adapids and omomyids) were obviously very primitive, and Le Gros Clark (1934, p. 22) concluded that they could only be characterized by their incorporation of "potentialities for evolutionary development along certain definite lines." The word "potentiality," or potential, has always

represented a key concept in discussions of homoplasy, indicating the idea that the generative basis of morphological traits can be maintained even when the traits themselves are absent.

Because early primates were so primitive, Le Gros Clark felt the need to diagnose the order based on derived features seen in later taxa, calling them "prevailing evolutionary tendencies." These parallel trends began with prosimian-like creatures and reached full expression in anthropoids: enhancement of free mobility of digits, especially the thumb and toe; progressive abbreviation of snout or muzzle; elaboration and perfection of visual apparatus, especially binocular vision; reduction of sense of smell; and progressive expansion and elaboration of the brain.

With the development of the neodarwinian synthesis in the 1940s and 1950s, the concept of orthogenesis as a law-like source of nonadaptive trends in evolution was largely abandoned. For example, Rensch (1959) recognized orthogenetic patterns, but regarded these as ultimately the result of a combination of mutation and natural selection. The view remained that extensive adaptive trends characterized primate and human evolution. Most researchers, such as Schultz (1951) and Straus (1949), continued to argue that the similarities between humans and living apes were the result of parallelism. The main opponent of these views was Washburn (e.g., 1951, 1968) who followed Gregory in arguing for a derivation of humans from an African ape ancestry because of shared anatomical similarities.

With the expansion of the primate fossil record in the 1960s and 1970s, particularly through the efforts of Elwyn Simons, the significance of parallelism in primate and human evolution took a decidedly different turn. In the approach of Simons, Louis Leakey, Pilbeam, and many others during this time, emphasis was placed on identifying unique features of modern taxa in fossils, without undue concern for the implications this may have for parallel evolution or reversals in other features. *Ramapithecus* and even *Propliopithecus* were identified as early hominids because of canine reduction. *Pliopithecus*, *Limnopithecus*, and *Dendropithecus* were considered to be ancestors of

gibbons, and different species of "*Dryopithecus*" from the Miocene of Africa were thought to give rise to chimpanzees and gorillas. These ancestor-descendant relationships often implied extensive parallelism in the evolution of postcranial features and other aspects of anatomy in living taxa, but this consequence was rarely discussed. Comparative anatomists such as Schultz, Straus, and Le Gros Clark had already spent previous decades providing an explanatory basis for extensive parallel evolution in modern apes, so the implications of ancient, generalized ancestors for modern taxa came as no surprise (see review in Fleagle and Jungers, 1982).

It is worth emphasizing that although parallel evolution was still prevalent in primate (and particularly anthropoid) phylogenies proposed during this time, these parallelisms did not involve assumptions of orthogenesis or the explicit recognition of trends. Instead, hypotheses of parallelism resulted from emphasizing particular traits to the exclusion of others, and on using particular ancestral fossil taxa to date divergences of modern clades. Again, it was Washburn (e.g., 1968) and his students (Corruccini et al., 1975, 1976, 1980) who repeatedly pointed out that these fossil phylogenies based on dental similarities between particular "Miocene apes" and living hominoid genera implied tremendous parallel evolution of postcranial similarities among modern hominoids. As they documented, the "Miocene apes" generally lacked any of the "brachiating" adaptations shared by living hominoids. Instead, Washburn, Corruccini, and others argued for what they considered to be a more parsimonious phylogeny: a clade of Miocene apes preceding the radiation of living hominoids. This view in many ways laid the groundwork for current understanding of fossil hominoid relationships (see volumes edited by Ciochon and Corruccini, 1983; Begun et al., 1997).

While debates such as these occupied anthropologists through the 1970s and 1980s, cladistics was becoming increasingly refined as a methodology for discovering phylogenetic relationships. A result of this trend was a strict avoidance of a priori identification of parallel evolution in phylogenetic reconstruction (Wiley, 1981; Eldredge and

Cracraft, 1980; Patterson, 1982; Farris, 1983). "True" similarity, meaning synapomorphy, and misleading similarity came to be more firmly distinguished in phylogenetics, and homoplasy of any kind took on the connotation of misleading information. Hennig (1966) explicitly recognized that explaining homoplasy was not necessary in phylogenetics, as in the following:

The question of how parallelisms in the narrow or broad sense are to be explained genetically is not of such great importance to phylogenetic systematics, for which it is a question of finding criteria that make it possible to decide whether or not the occurrence of identical characters or whole character complexes in different species is based on the fact that these were taken over from one stem species that is common only to these species (synapomorphy)" (Hennig, 1966, p. 119).

Thus explanations of homoplasy were excluded from phylogenetics. Because of the general utility of convergence in studying adaptation, homoplasy in the cladistic era still served as a post hoc basis for understanding evolutionary process, usually by researchers other than those studying relationships. The role of trends and parallel changes had become radically different from the situation during the first half of the century, during which time parallel evolution was an *expectation* rather than a secondary phenomenon.

Anthropologists were slow to adopt rigorous cladistic practice, and early applications of phylogenetic systematics to primate and human evolution mostly consisted of gathering morphological data to support a preferred cladogram rather than performing any formal analysis (see papers in Grine et al., 1987). Despite the lack of rigorous computer searches for the most parsimonious cladograms, it was already clear that homoplasy was common and complex in primates, and might prohibit the easy identification of accurate phylogenies (e.g., Eaglen, 1983; Ford, 1986). For many researchers, homoplasy was generally seen as the result of error due to bad choice of characters and misidentified homology. However, the "reality" of homoplasy can be seen in the effect that fossil discoveries have had on phylogenies in recent years. Whether phylogenetic systematics is practiced formally or informally, it has become common for fossil

taxa to be found that belong to a particular clade based on selected data sets or traditional "key" characters, but at the same time reveal parallel evolution among various other traits, hitherto thought to be synapomorphies. In other words, the combination of traits in the fossil taxon sets up a situation where one body of evidence (e.g., cranial, dental, or postcranial) is substantially homoplastic, and it is unclear which data set to prefer (e.g., *Sivapithecus* in hominoids: Pilbeam et al., 1990; Ward, 1997; Larson, 1998). These situations have demonstrated that homoplasy is "rampant" and led to some agnosticism with regard to specific questions of phylogeny and the general application of cladistic methodology.

Homoplasy has also gained visibility as phylogenetic analyses in primate and human evolution have become increasingly complex. Computer programs that are now available permit analyses of large data sets (numbers of taxa and characters) that often generate numerous equally parsimonious trees. Statistics such as consistency (CI) and retention (RI) indices are readily calculated to express the proportion of character change that reflects homology or homoplasy. The utility of these indices is debated (Sanderson and Donoghue, 1989, 1996; Archie, 1996), but they do serve to attach a number to observations of extensive homoplasy in primates and other groups. A homoplasy index is determined as the complement of the CI, and Table 1 summarizes homoplasy indices for a number of primate cladistic analyses. These indices are similar to those expected from patterns in other groups (Sanderson and Donoghue, 1989). Primates do not exhibit unusually high or low levels of homoplasy, and within primates, no single type of data appears to be less homoplastic than other types of data (see also Sanchez-Villagra and Williams, 1998).

Greater analytical sophistication in the study of phylogeny has not eliminated homoplasy, and neither have further fossil discoveries. Instead, the topic has only become more conspicuous. As it has been throughout the last two centuries, homoplasy remains an important subject relevant both to those seeking an accurate depiction of primate phylogeny as well as those attempting to

understand the processes that generate evolutionary change (e.g., Lieberman et al., 1996; McHenry, 1996; Fleagle, 1997; Larson, 1998; Lockwood, 1999; Wood, 1999).

DEFINING HOMOPLASY

Homoplasy is usually defined and discussed with respect to homology. Both terms can be defined using phylogenetic pattern, morphological structure, developmental basis, and various other methods. In this section, we discuss a variety of views, beginning with a relatively straightforward definition based on pattern, wherein homoplasy and homology are clearly distinct, and finishing with a consideration of how alternative definitions of homology and homoplasy relate to the level of analysis. When multiple levels of analysis are incorporated, the definition of homology or homoplasy becomes more complex, and the two terms less clearly separated.

Homology, homoplasy, and definition by pattern

Definitions of homology are much like species concepts; most biologists have an idea what homology is and recognize its fundamental importance, but a universal criterion for identifying homology is impossible to achieve except by reference to the distribution of characters and taxa on a phylogenetic tree (Fig. 1). Thus most biologists today have adopted an operational, post hoc definition of homology based on patterns of character distribution: homology is similarity shared by any number of taxa that is present in their last common ancestor (e.g., Lauder, 1994).

Along the same lines, homoplasy is similarity shared by taxa that is not present in their last common ancestor — the converse of homology. In this sense, no homoplastic structure can be homologous at the same time, regardless of structural similarity or developmental basis. This condition forms the basis of phylogenetics and applies only *within a single analysis*, as different character definitions or level of study may indeed change the status of a structure from homoplastic to homologous, and vice versa.

Alternatively, homology can be defined with reference to various anatomical crite-

TABLE 1. Quantifying homoplasy in various cladistic analyses of primates¹

Group of interest	No. of taxa	No. of characters	Homoplasy index ²	Expected homoplasy index ³	Type of data	Source
Archonta	11	154	0.37	0.32	Craniodental, postcranial, soft tissue	Simmons (1993)
Archonta	23	33	0.41	0.49	Cranial	Kay et al. (1992)
Primates	38	34	0.39	0.63	Behavioral	Di Fiore and Rendall (1994)
Strepsirhini	34	86	0.60	0.60	Cranial, dental, postcranial, soft tissue	Yoder (1994)
Anthropoidea, related taxa	57	291	0.57	0.66	Cranial, dental, postcranial, soft tissue	Ross et al. (1998)
Anthropoidea, related taxa	33	157	0.63	0.59	Dental	Kay and Williams (1994)
Anthropoidea, related taxa	17	42	0.44	0.41	Cranial	Ross (1994)
Anthropoidea, related taxa	11	33	0.20	0.32	Postcranial	Dagosto and Gebo (1994)
Anthropoidea, related taxa	15	18	0.42	0.38	Cranial	Beard and MacPhee (1994)
Anthropoidea	9	66	0.13	0.28	Dental, cranial, postcranial	Fleagle and Kay (1987)
Platyrrhini	17	66	0.44	0.41	Mainly craniodental	Horovitz and Meyer (1997)
Platyrrhini	19	117	0.55	0.44	Dental	Kay (1990)
Hominoidea	11	55	0.32	0.32	Postcranial	Ward (1997)
Hominoidea	8	79	0.15	0.26	Cranial, dental, postcranial	Begun and Kordos (1997)
Hominoidea	8	240	0.37	0.26	Cranial, dental, postcranial	Begun et al. (1997)
Hominini	11	60	0.35	0.32	Craniodental	Strait et al. (1997) ordered
Hominini	11	60	0.28	0.32	Craniodental	Strait et al. (1997) unordered
Hominini	7	77	0.28	0.24	Craniodental	Skelton and McHenry (1992)
Hominini	9	48	0.32	0.28	Craniodental	Lieberman et al. (1996)
Hominini	8	90	0.29	0.26	Craniodental	Chamberlain and Wood (1987)
<i>Homo</i>	9	11	0.26	0.28	Craniodental	Stringer (1987)

¹ Analyses of morphological data where consistency indices (CIs) were reported, enabling calculation of a homoplasy index. For the most part, CIs were for the most parsimonious tree for the data set, and not necessarily a "known" or preferred tree. Where multiple analyses were performed under different assumption sets or alternative taxonomic designations, the highest CI is used.

² The homoplasy index (HI) is the proportion of character change in a data set that is homoplastic for a phylogenetic tree and is simply the complement of the CI ($HI = 1 - CI$); (Archie, 1996). Higher numbers indicate more homoplasy, and the HI tends to increase with larger numbers of taxa (see footnote 3). The CI is minimum number of steps summed across all characters in a data set divided by the actual number of steps on a phylogenetic tree.

³ These "expected" HIs are calculated based on the number of taxa in the analysis, using the formula for expected CI from Sanderson and Donoghue (1989). That formula was derived from a regression analysis of CI on the number of taxa for cladistic analyses of various plants and animals.

ria (e.g., Remane, 1952; Boyden, 1973), the mechanistic basis for character expression, such as developmental pathways (Nelson, 1978; Roth, 1984; Lieberman, 1999), or genetic substrates (discussed in Meyer, 1999; Wray, 1999). These methods seek to identify homologies without reference to a phylogenetic tree, and are helpful in making a priori statements of similarity prior to using characters in a phylogenetic analysis. But as clearly documented in Hall's (1994) edited

volume, each of these criteria ultimately fails to provide consistent criteria for homology, mainly because they can conflict with each other (also De Beer, 1971; papers in Bock and Cardew, 1999).

For example, among congeneric species of amphibians, there is variation as to whether differentiation of the cornea and lens of the eye is induced by interaction with the optic vesicle or occurs independently (Hall, 1992). But the lens itself is structurally homolo-

gous across species despite different modes of development. In primates, Yoder (1992, p. 194) established that the ascending pharyngeal artery shared by cheirogaleid and lorisooid strepsirrhines "passes all known a priori tests of homology," including that of development (Yoder, 1992). However, this feature appears to be homoplastic in Yoder's (1994; Yoder et al., 1996) later reconstructions of phylogeny based on a combination of genetic and morphological data. Thus, homologous traits may have a different developmental basis, while homoplastic traits may have the same developmental basis (see also the examples in Lieberman, 1999).

Despite the apparent failure of such "process" definitions of homology, many biologists feel that there is more to homology than congruence on a cladogram. Different definitions of homology permit the observation that structurally or developmentally homologous features can be phylogenetically homoplastic. Rather than producing confusion, this situation may highlight a way in which different kinds of homoplasy can be distinguished from each other, namely, that some *homoplastic* features can reflect *homologous* similarities at a different level of analysis (Fig. 4, discussed further below). Perhaps the most common example of this reasoning is the idea that parallelism and convergence are different phenomena.

Parallelism and convergence

Comparative biologists have distinguished between parallelism and convergence for as long as they have recognized homoplasy, and in many cases they have preferred using one or both of the terms instead of "homoplasy." By distinguishing parallelism and convergence, one separates types of homology based on the process by which the traits come about.

Convergence is usually defined as a basic functional similarity achieved by structures that are different in detail, such as the wings of birds, bats, and insects — in other words, a similar result from a different ancestral starting point. In contrast, parallelism is conceived as detailed similarity achieved in the same manner by related taxa, for example, the prehensile tails of capuchin monkeys and spider monkeys, or the fused mandibles of some indriids and anthropoids.

Convergent structures such as bat wings and insect wings may be formed by nonhomologous elements, whereas, for example, the prehensile tails of capuchins and atelines are formed of homologous bones (caudal vertebrae) and muscles, in the structural and developmental sense of homology. Hennig (1966) saw parallelism as a very frequent occurrence, with convergence rare and less obstructive to phylogenetic analysis. Lieberman (1999, p. 147) described parallelism as "an especially pernicious form of homoplasy because the similarities are, by definition, developmentally homologous."

Patterson (1982) explained parallelism and convergence in terms of three criteria of homology: conjunction, similarity, and congruence. In brief, conjunction requires that homologous structures not be repeated in the same organism. Similarity is meant in a fairly strict sense: "topographic, ontogenetic, compositional" (Patterson, 1982, p. 21). Congruence represents precisely the pattern definition of homology described above: A trait is homologous in a phylogeny if it is shared by a group consistent with that phylogeny, and homoplastic if it is not. Congruence derives from Hennig's (1966) method of recognizing homoplasy, and according to Patterson (1982), this criterion is the ultimate arbiter of a character's status as homology or homoplasy.

Using these criteria, parallelism fulfills the criteria of conjunction and similarity, but not congruence. Convergent traits fulfill only the criterion of conjunction. Because they fail to exhibit detailed similarity, convergent traits are presumably recognized as *different* traits prior to a phylogenetic analysis. If coded differently, convergent characters are not even homoplasy in the strict sense used in a phylogenetic analysis, because homoplasy implies close enough similarity to mislead the analysis. Parallelism, on the other hand, is expected to be misleading, and falls much more in line with homoplasy in the operational sense. It is a sign of the potential confusion of these terms that many workers use convergence as a synonym of homoplasy and dismiss the concept of parallelism altogether, in opposition to what Patterson's (1982) criteria would suggest (see below).

Although concepts of parallelism and convergence seem to have logical boundaries, many have pointed out that in practice they can grade into one another. This is simply because all homoplastic traits are similar on some level, and therefore the criterion of similarity is difficult to use objectively. Bird wings and insect wings are vastly different structures, but bird wings and bat wings have some elements in common, with others being modified in different ways. How much of the developmental pathways and genetic code is the same is unknown for most structures, but the increasing literature on Hox genes indicates that even analogous structures such as bird wings and insect wings do have genetic components in common (Shubin et al., 1997; Meyer, 1999).

This problem led Eldredge and Cracraft (1980) to suggest a more objective definition of parallelism based on patterns of character evolution on a cladogram. They defined parallelism as homoplasy in two sister groups, that is, the evolution of the same character state in branches diverging from the same node on a cladogram (Fig. 3). This can also be referred to as sister-group homoplasy. Convergence is all other homoplasy. Although potentially interesting, parallelism as sister group homoplasy is difficult to recognize without detailed knowledge of population histories, and it does not constitute misleading evidence like other kinds of homoplasy (Wilkinson, 1991). By treating all misleading cases of homoplasy as convergence, Eldredge and Cracraft (1980) come to precisely the opposite conclusion of that implied by Patterson's (1982) criteria of homology.

Difficulties in distinguishing between parallelism and convergence epitomize the difficulty of consistently defining homology and homoplasy. Parallelism and convergence have no place in a world of homoplasy recognized only by pattern of congruence. However, these concepts have heuristic value in understanding why homoplasy occurs. Although the terms are old, they illustrate very well the modern dilemma of making absolute statements about trait similarity when growing evidence indicates that the pattern of similarities for a morphological structure may vary depending upon the

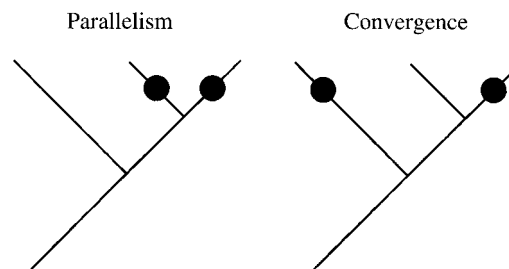


Fig. 3. Parallelism and convergence as defined by Eldredge and Cracraft (1980). Most workers defined these events in terms of the processes by which similarity is achieved or the degree of relatedness of the taxa showing homoplasy. Eldredge and Cracraft (1980) took the latter view and made it objective by defining parallelism as homoplasy in two sister groups, and convergence as all other homoplasy. Note that in this case parallelism is nearly impossible to detect, as parsimony would suggest that the trait arises only once, below the node where the sister groups diverge.

biological level at which that structure is studied (e.g., Lauder, 1994; Abouhief, 1997; Meyer, 1999).

Levels of analysis

Nonphylogenetic definitions of morphological homology tend to refer to processes at levels other than adult similarity. The inconsistency of these definitions has led to a recent trend to separate more clearly than before the different levels at which traits are characterized (Wake, 1996, 1999; Wray, 1996, 1999; Brooks, 1996; Meyer, 1999), but this recent trend essentially hearkens back to earlier workers who recognized the problem before underlying mechanisms were understood (Rensch, 1959; Remane, 1961; Hennig, 1966; de Beer, 1971). Various levels of analysis can be specified, including adult morphology, adult behavior, morphology or behavior at different stages of growth, components or microstructure of morphological features, and genes. Because similarities at different levels of analysis have been shown to vary independently, Müller (in Bock and Cardew, 1999, p. 44) recommended that, "We must not define homology at one level via mechanisms that belong to a different level of analysis." This argument goes against the traditional view that different patterns of development or genetic bases can be used to identify nonhomologous structures.

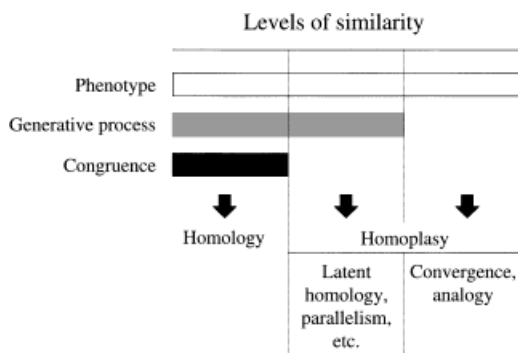


Fig. 4. This schematic diagram illustrates that when underlying *processes* are used to define homology and homoplasy, the division between the two is not clear-cut. Even though homoplastic traits exhibit incongruence with a phylogenetic tree, they may derive from the same developmental or genetic basis (generative process), and are therefore "homologous" at a different level. In other words, the common ancestor may possess the potential, or capability, to express a trait shown by some descendants. Recognition of this has led to terms such as those listed in Table 2.

Along this line of reasoning, it may be that simple pattern definitions of homology and homoplasy suffice, and any two characters, be they adult phenotypes, developmental stages, gene sequences, etc., can be subject to the test of congruence to determine whether they are homologous. The principal guideline would be to separate different levels of analysis for a particular feature, from its genetic basis to its adult phenotype, and not to judge form at one level to be nonhomologous simply because form at another level is nonhomologous.

An alternative way of portraying the levels problem follows from the idea that underlying genetic or developmental mechanisms for producing adult phenotypes can be retained whether these phenotypes are expressed or not, and that patterns of homoplasy are produced when mechanisms are "switched on and off" or when thresholds of development are crossed to produce a qualitatively different trait (Fig. 4, and Meyer, 1999). This concept has deep roots in studies of morphology and paleontology, and many different workers have suggested ways of understanding homology as applied to parallel evolution. For example, consider the types of homoplasy listed in Table 2. These phenomena were suggested by various biolo-

TABLE 2. Various concepts illustrating the "middle ground" between homology and homoplasy¹

Latent homology (de Beer, 1971): homoplastic expression of two similar traits via a morphogenetic system that is retained but not used in the common ancestor (or used for some other purpose).
Homoiology (Remane, 1961): homoplastic characters arising through similar epigenetic processes operating on a genetic basis inherited from a common ancestor.
Underlying synapomorphy (Tuomikoski, 1967, Saether, 1983): "parallelism as a result of common inherited genetic factors."
Parallelism (Simpson, 1961:78): "the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry."
Apomorphic tendency (Cantino, 1982): derived feature present in some but not all members of two or more higher taxa that is indicative of genetic affinity among those taxa.

¹ See also Figure 4.

gists based on phylogenetic patterns of morphology prior to recent work in genetics and developmental biology, and include terms such as latent homology (de Beer, 1971), homoiology (Remane, 1961; Hennig, 1966), underlying synapomorphy (Tuomikoski, 1967; Saether, 1983), parallelism (e.g., Simpson, 1961), and apomorphic tendency (Cantino, 1982).

Parallelism is, of course, the most common term used in reference to concepts such as these, as reviewed above. Hennig (1966) used parallelism and homoiology interchangeably. To what extent these several terms mean the same thing depends on interpretation; there is room for difference as to whether the developmental or genetic basis of the traits is the focus of their definition or whether either is specified. But all appear to have the same goal, which is to describe a situation in which two taxa show a trait that is essentially "the same" in every sense although it is not present in their common ancestor. This sameness presumably results from a shared mechanism of expression.

There seems to be little doubt that these concepts are theoretically valid in many cases of homoplasy and can be documented in studies of genetic mechanisms (e.g., Wray, 1999; Meyer, 1999). At issue is the extent to which they can be distinguished from other types of homoplasy. Those who believe that parallelisms or any of the phenomena

listed above can be phylogenetically meaningful would include both homology and latent homology in the category of meaningful similarity (Gosliner and Ghiselin, 1984; Saether, 1983; Sluys, 1989). Others would simply refer to latent homology or homoiology as phylogenetically meaningless homoplasy and dismiss it (e.g., Eldredge and Cracraft, 1980), or argue that although theoretically interesting, these concepts cannot be recognized in a practical way (Patterson, 1982). The latter views are more common with regard to phylogenetic reconstruction.

Again, reconciling divergent views of cases in which homoplasy reflects a shared mechanism of expression requires separation of the levels at which traits are studied. Patterns expected based on concepts of latent homology or underlying synapomorphy are certainly present in many different organisms (Sluys, 1989; Wake, 1996, 1999; Brooks, 1996; and see below). While the phenotypic expression of these traits is homoplastic and not informative regarding phylogenetic relationships, these particular cases of homoplasy highlight similarities at another level, usually genetic or developmental, that may be homologous and indicative of phylogeny.

Probably the main difficulty in incorporating some concept of latent homology into comparative biology is the lack of information about generative processes in most organisms being studied. In fact, Eldredge and Cracraft (1980) explicitly dismissed the concept of parallelism in part because of its reliance on assumptions about generative processes giving rise to homoplastic traits. Since their book was written, much more has been learned about the production of phenotype, and this is probably responsible for concepts such as latent homology being revived (see discussions in Bock and Cardew, 1999).

While further understanding of generative processes is certainly a promising area of research in understanding homoplasy, it should also be recognized that generative processes include an array of topics for which we already have fairly detailed knowledge (Schlichting and Pigliucci, 1998). In primates, areas such as allometry and functional relationships among traits are well known and may produce patterns of homo-

TABLE 3. *Factors in morphological homoplasy*

Methodological homoplasy	Biological homoplasy ¹	
	Intrinsic factors	Extrinsic factors
Mistaken homology (inadequate character analysis)	Developmental constraint/potential	Adaptation, natural selection
Parsimony ²	Genetic constraint/potential Structural relationships (e.g., allometry)	Epigenetic response to external conditions Behavioral plasticity, "learning"

¹ For heuristic purposes, we divide biological homoplasy into sources based on intrinsic and extrinsic factors, but these are not entirely separate domains.

² Parsimony is a "factor" in homoplasy because it operationally minimizes homoplasy in phylogenetic analysis and makes certain assumptions about homoplasy.

plasy that suggest concepts like latent homology. Some examples are discussed below.

In summary, the complex array of definitions of homoplasy can be distilled down to two major categories. Many researchers, particularly phylogenetic systematists, see "cladistic" homoplasy, defined solely by incongruence with a phylogenetic tree. Others see "evolutionary" homoplasy as a broad phenomenon due to many processes that are conceptually and sometimes practically distinguishable. The latter view is implied whenever the phrase "homoplasy because of . . ." is used. Subsequent sections address both of these views, for they are not mutually exclusive. To a large extent, one's definition of homoplasy depends on research interest. Therefore, it comes as no surprise that divergent views exist, as similar differences in opinion exist for other major concepts in the study of evolution, such as species definitions (e.g., Eldredge, 1993; de Queiroz, 1998) and adaptation (Reeve and Sherman, 1993).

METHODOLOGICAL FACTORS IN HOMOPLASY

It is possible to subdivide in many ways the factors that influence homoplasy, but the most important is to separate methodological homoplasy from biological homoplasy (Table 3). The former is tied to aspects of character analysis and the phylogenetic analysis itself, while the latter is comprised of causes of homoplasy as well as opportuni-

ties for inferences to be made about macro-evolutionary processes from patterns of homoplasy.

Character definition

No matter how a phylogenetic analysis is conducted, it is preceded by a process of character definition that breaks down suites of morphology into component units of information. Characters take many forms, from more or less atomized qualitative features to a series of measurements or ratios of shape. To conduct a phylogenetic analysis, characters must be categorized in a way that identifies the same or similar features in different taxa. These statements of similarity are actually a priori hypotheses of homology, and typically anatomical criteria of homology, such as those outlined by Remane (1952) are applied. They are only hypotheses of homology, because in a phylogenetic sense, characters are not shown to be homologous until they have passed a test of congruence on a phylogenetic tree. In short, character definition seeks to divide morphology into a meaningful suite of characters, and then establish which of these characters exhibit "sameness" (Wake, 1999) among traits (see Lieberman, 1999, for some qualities of "good" characters).

Homoplastic traits must exhibit "sameness" at some level. Methodological homoplasy can result simply from error in statements of similarity between two traits. Character analyses may be superficial, or conservative with regard to how finely the morphological traits are divided. Practical problems, such as fossil preservation, or poor sample size, may lead to insufficient knowledge of dissimilarity between two traits that are initially coded as homologous. Conservatism in splitting traits at the outset may be a useful strategy, often leading to reexamination of homoplastic traits and revised statements of similarity. Changing definitions post hoc, once a character is "known" to be homoplastic, serves to turn one homoplastic trait into two separate traits, each of which satisfies tests of congruence. However, there is a possibility in this case of increasing the support for an incorrect phylogenetic tree. With the inclusion of more data and/or taxa, some homoplastic

traits may eventually be shown to be homologous. Therefore, defining away homoplasy should be done cautiously, if at all.

It is clear that statements of homoplasy depend very much on character definition, and this can be a subjective enterprise. Cartmill (1982b) demonstrated how the same morphological space can be categorized in different ways, possibly leading to different phylogenetic hypotheses. Preference of one phylogeny may lead a researcher to define traits in a particular way that leads to support for that phylogeny. It is also true that character analysis can involve the explicit rejection of certain traits which are "known" a priori to be homoplastic. Such a decision probably provides the greatest opportunity for bias to creep into a phylogenetic hypothesis.

An example of how character definition can affect interpretations of homoplasy is the prehensile tail of some New World monkeys. A prehensile tail occurs in five genera: *Cebus*, *Alouatta*, *Ateles*, *Lagothrix* and *Brachyteles*, the latter four of which comprise the subfamily Atelinae. The tail can be characterized in several ways: the same character state in all five genera; two character states, with one representing several specializations of the tail that characterize atelines; and numerous characters, with the "tail" broken down into various elements of length, vertebral structure, muscle mass and organization, and skin surface. Since *Cebus* is now widely accepted not to be closely related to atelines, the character state "prehensile tail" must be homoplastic (e.g., Rosenberger, 1983; Ford, 1986). In fact, the prehensile tail is widely cited as an example of homoplasy, and has given rise to theories of preadaptation in New World monkeys (Rosenberger, 1977) and hypotheses about how forest canopy structure influences tail evolution (Emmons and Gentry, 1983).

However, if the morphology of the tail is defined in a way that distinguishes *Cebus* and atelines, the trait is not homoplastic. Among taxa with tails, Horovitz and Meyer (1997, p. 223) distinguished two states: "tail present without glabrous surface," and "tail present with glabrous surface." *Cebus* does not have a glabrous surface on its tail and

therefore shares the primitive condition with all New World monkeys other than atelines. Defined in this way, one of the more commonly recognized homoplastic traits in primates does not exist and the distribution of character states in the tail is perfectly congruent with the most parsimonious phylogeny.

Finally, if Ankel's (1972) detailed study of tail morphology is followed, the trait "prehensile tail" becomes a nebulous concept (see also Rosenberger, 1983). The tails of *Cebus* and the atelines differ in so many ways that finely divided characters might not suggest this functional similarity between them.

Another example is the presence of hypocones in Eocene adapoids. The common ancestor of the North American notharctines and the European adapines lacks a hypocone. However, many later members of both groups have a hypocone. This presence of a hypocone in the two groups has been used to argue for a close relationship between the two subfamilies (e.g., Gregory, 1920). However, it is clear that the hypocone develops differently in the two groups, raising the possibility of nonhomology. In notharctines it forms as a division of the protocone and is often called a pseudohypocone, while in adapines it develops from the lingual cingulum. If this structure is identified as a hypocone, it is a case of homoplasy in the two groups, but if one is identified as a hypocone and the other a pseudohypocone, then no homoplasy is involved.

In some cases, important phylogenetic debates hinge on the definition of a few characters. For example, the identity of the sister group of anthropoids has inspired fierce debate over character structure and similarity. Two traits, the postorbital septum and the anterior accessory cavity and surrounding petrosal structures, are argued by some to be homologous in tarsiers and anthropoids, despite some differences in detail (MacPhee and Cartmill, 1986; Ross, 1994). Others focus on these differences and assign different character states to the two groups (Rosenberger and Szalay, 1980; Simons and Rasmussen, 1989). Not coincidentally, the latter authors do not favor a tarsier-anthropoid clade.

There is no definite resolution to this debate. However, it is clear that at some level the postorbital septum and anterior accessory cavity of the middle ear can be argued to be similar in anthropoids and tarsiers, and therefore homoplastic if tarsiers and anthropoids are not sister groups. But as with the prehensile tail, the "sameness" can be defined away if the differences, rather than similarities, are emphasized in character definition.

Thus, patterns of homoplasy derive from how traits are defined. Broad definitions of characters will increase apparent degrees of homoplasy, whereas strict definitions will eliminate some cases of homoplasy. However, a compromise approach is needed, because overly strict definitions may also eliminate evidence of synapomorphy.

Character analysis is not limited to establishing the similarities or differences among traits. Numerous other issues arise even after characters have been defined, among them character independence, polymorphism, missing data, character weights, etc. Simmons (1993) has extensively reviewed these concerns as they pertain to the results of phylogenetic analyses of Archonta — the group comprised of primates and their close relatives.

Character independence is an especially prominent consideration in character analysis, although it is usually dealt with implicitly. Some suspect that phylogenetic studies of hominin evolution have been led astray by suites of correlated, homoplastic traits related to masticatory function (Skelton and McHenry, 1992; McCollum, 1999). Whether or not that is the case, there is no reason to expect that homoplastic traits are more likely to be redundant with each other than are homologous traits. All characters, whether they appear homologous or homoplastic on the preferred tree, should be investigated for independence. Problems of character correlation only affect inferences of homoplasy in so far as they affect the result of the phylogenetic analysis. Character correlation is not a "cause" of methodological homoplasy. This is true also of other analytical concerns such as how to deal with polymorphism or missing data. Patterns of homoplasy depend very much on the preferred phylogenetic tree, but

most analytical choices in a phylogenetic analysis do not directly lead to homoplasy.

To sum up, methodological homoplasy occurs primarily when characters that are actually "different" are considered a priori to be the "same" and then appear as parallel or convergent similarity in a phylogeny. This can be viewed as an error or a decision to focus on a broad level of similarity. Other methodological problems in character analysis, such as redundancy of character definitions, introduce error into the phylogeny but only indirectly affect homoplasy by affecting the choice of phylogenetic tree.

Parsimony, homoplasy, and extrinsic sources of evidence

While character analysis is without doubt a central phase of phylogenetic analysis, and presumably where "mistakes" of homoplasy occur, the computational analysis that follows also introduces a methodological philosophy concerning homoplasy. The current paradigm of phylogenetic analysis, particularly as applied to primate morphology, is dominated by the use of parsimony-based analyses of character distributions.

In a parsimony analysis, homoplasy is the feature that parsimony seeks to minimize. Homoplasy represents conflicting evidence that has been dismissed, and this dismissal requires an *ad hoc* hypothesis, of which there should be as few as possible (Farris, 1983). Farris (1983) used the analogy of regression analysis to explain why no amount of homoplasy can validly be used to criticize the method of minimizing homoplasy through parsimony. A linear least squares regression minimizes the amount of residual variance relative to that line, just as the most parsimonious phylogenetic hypothesis minimizes the amount of homoplasy present in the phylogeny of a group. In a regression, the line that provides the best fit will be the same no matter how much residual variation occurs, as long as that residual variation is distributed in an unbiased way. Farris (1983) argued that increased amounts of homoplasy *do not* affect the choice of phylogenetic tree in the same way that increased amounts of residual variation *do not* affect the choice of regression line. Following on the same analogy,

Coddington (1994, p. 59) referred to homoplasy as "the 'error' term in cladistic analysis."

However, this analogy also reveals the reason why many researchers are uncomfortable with parsimony-based analyses. Linear regression analysis, like any statistical method, does come with some assumptions. Mainly, it assumes that the data can be explained (in part) by a linear relationship. Likewise, parsimony analysis assumes, among other things, that "one conclusion of homoplasy does not imply others" (Farris, 1983, p. 35), i.e., that homoplastic traits are not directed in an ordered way that would favor an incorrect phylogeny. Considering the wide variety of forces that may direct homoplasy, i.e., the biological sources of homoplasy that we discuss below, this assumption may seem problematic. Unfortunately, while regression analysis is self-correcting in the sense that undesired patterns in residual variation are easy to identify, parsimony analysis does not yet have a corresponding ability.

Potential problems with parsimony lead many to be suspicious of rigid adherence to these techniques. But if not parsimony, what? One way of addressing that question is to consider parsimony as it is defined with respect to types of data other than morphological characters. The criterion of simplicity is of undoubted utility in science, and some cladistic theoreticians would extend the application of parsimony to properties of organisms that are extrinsic, such as geographic location and occurrence in time (Sober, 1983, 1988; Kluge, 1997). Sober states (1983, p. 40):

We might imagine a simplicity ordering of possible hypotheses. We move from simpler to more complex alternatives, and accept the first one that passes the test of observation and experiment (and consistency with other theories, of course).

These "other theories" explicitly include "checking phylogenetic hypotheses against biogeographic data" (Sober, 1983, p. 45). This particular example may be anathema to those seeking to test biogeographic hypotheses with character distributions. But the point is that parsimony in character distributions is just one aspect of an overarching

criterion of simplicity. Such a broad view seems to open the door for many recent trends in phylogenetics, including the use of temporal distributions of fossil taxa (Fisher, 1994; Huelsenbeck, 1994; Wagner, 1998; Fox et al., 1999) and the desire to corroborate phylogenies with hypotheses of functional morphology (Lee and Doughty, 1997; Begun and Kordos, 1997; Ravosa, 1999; Ross, 1999; see also Gosliner and Ghiselin, 1984). A vexing question is how to weight the contribution of character data and other sources of information. Character data cannot be considered totally secondary to biogeography or stratigraphy. In many cases, character distributions may provide evidence that seemingly unlikely migration events have taken place, a particular fossil record is poor, or the functional hypothesis for character evolution is incorrect.

This difficulty is similar to that discussed in an ongoing debate over how to combine the cladistic results from different types of character data, particularly those, such as genetic sequences and morphological characters, that evolve under different sets of processes (e.g., Barrett et al., 1991; Bull et al., 1993; Chippindale and Wiens, 1994; Miyamoto and Fitch, 1995). The recognition of homoplasy will always be facilitated by comparing the hypotheses supported by different sources of evidence, but methods of choosing a particular hypothesis based on combined data increase the methodological complexity of phylogenetic analysis.

In short, the methodological significance of parsimony-based analyses to the study of homoplasy is twofold. Parsimony analyses of character data alone prevent some detection of homoplasy, since they are founded on the principle that homoplasy is to be minimized. On the other hand, applying a broad principle of parsimony to different lines of evidence, and not only character data, can reveal homoplasy if the results of separate analyses are incongruent.

BIOLOGICAL FACTORS IN HOMOPLASY

Biological explanations of homoplasy are necessary when the homoplasy is "real" and identical features not found in the common ancestor appear in separate lineages. As reviewed above, homoplasy is more consis-

tently defined by pattern than process. But a given pattern of homoplasy is potentially explainable by several alternative processes, and these alternatives serve as the basis of discussion for much of the rest of the paper. Several topics are presented, some with primary relevance to phylogenetic questions, others with more relevance to questions of adaptation.

One way of examining the processes underlying homoplasy is to divide them into intrinsic and extrinsic factors (Table 3). Homoplasy resulting from intrinsic factors is based on properties of the organisms in the clade of interest. This is often labeled "constraint," whether that be developmental, genetic, structural or otherwise. Wake (1991) argued that developmental constraints may be more important than extrinsic, ecological factors in explaining homoplasy. Like Gould and Lewontin (1979) and others, Wake (1991) cautioned that separate evolutionary events that lead to similar results do not always indicate a common adaptive explanation. Constraints on morphological evolution may lead to similarities that occur in response to selection for different properties, giving rise to a disjunction between structure and function.

Nonetheless, there is frequently a good relationship between behavior, the external environment, and patterns of homoplasy. This relationship is fundamental to studies that use the comparative method to develop explanations of adaptation (e.g., Kay and Cartmill, 1977; Kay and Covert, 1984). The independent repetition of events generated by homoplasy gives greater degrees of freedom to any analysis of association. In addition, it has long been suspected that "adaptive," or ecologically responsive, characters should be subject to homoplasy (e.g., Darwin, 1859; Eldredge and Cracraft, 1980). However, this statement is rarely addressed explicitly.

The problem with dichotomizing intrinsic versus extrinsic factors in homoplasy, or constraints versus natural selection, is that morphological expression very often represents a compromise between intrinsic and extrinsic forces. Nevertheless, this dichotomy provides a useful heuristic context for review-

ing the diverse processes that potentially influence homoplasy.

Constraints, evolutionary potential, and body plans

While *constraint* is probably the most common term used in reference to the principle that morphological features are more likely to occur in some organisms than others (Maynard-Smith et al., 1985; Reeve and Sherman, 1993; Schlichting and Pigliucci, 1998), it is also possible to express the same concept in terms of varying degrees of *potential* for certain morphological features (e.g., "canalized evolutionary potential," Saether, 1983). In this section, we discuss the effects of morphological constraints along with the concept of body plans, because the two areas of discussion are closely intertwined, and in some cases evidence for one is evidence for the other.

Constraints in evolution can be characterized in various ways. Some are dictated by physical laws, such as the relationship between cross-sectional area and volume (therefore body mass). Material properties being equal, a larger organism will usually have relatively thicker limb bones to maintain functional equivalence — the ability to support its own weight. This will not always be the case, particularly in comparisons across a narrow range of size, but deviations from the common pattern will be selected against.

A constraint commonly thought to produce homoplastic patterns is developmental constraint, wherein only a few developmental trajectories are "possible" from a particular starting point [see Wake's (1991) examples in salamanders]. In these cases, development is canalized so that small shifts in internal or external environment do not disrupt production of the adult form (Waddington, 1940, 1942). But given enough change in the external environment, a discrete shift to a different developmental trajectory can occur, producing an adult phenotype qualitatively different from the normal form. The effect is that a limited number of morphological outcomes are available, and, in a way analogous to the limitation of having only four nucleotides in genetic sequences, the recurrence of a particular form

is more likely. Indeed, homoplasy provides evidence that constraints have a significant effect on morphology (Wake, 1991; Schlichting and Pigliucci, 1998).

Morphological constraints and potentials relate closely to broader discussions of bauplans in evolution, because a constraint is often characteristic of a particular clade. The term "bauplan," or body plan, was incorporated into biology by Woodger (1945) and has seen relatively wide use as a concept for structural characteristics that unite a particular taxonomic group, in other words, a fundamental organization maintained and preserved within that taxonomic group (Valentine, 1986; Levinton, 1988; Valentine et al., 1996; Hall, 1992; Arthur, 1997).

With regard to homoplasy, or any expression of morphological change, two pertinent questions exist for the concept of body plans: Do body plans guide or constrain morphological evolution? If so, do body plans exist primarily at a particular level in the phylogenetic hierarchy, or are they nested within each other so that the effects are seen in patterns of morphological change at every level?

The latter question may be easier to answer. For example, Valentine (1986) and Hall (1992) both argue for a concept of nested, or hierarchical, body plans. The observation that many characteristic body plans are achieved in a stepwise fashion (e.g., the evolution of mammals) supports this view, as the body plan in this case merely comprises whatever characteristics have emerged to define a phylogenetic group at a particular moment in time. Eldredge (1989) expressed a similar view: body plans are equivalent to whatever suite of synapomorphies defines a monophyletic group and distinguishes that group from others. Interpreted this way, body plans appear to be a concept for recognizing simply that the current form of an organism determines to some extent the morphological changes possible in its descendants. Hence, body plans are often discussed in the same context as developmental and structural constraints.

The observation of body plans is usually an inference from patterns of character distributions. What is lacking is a clear understanding of mechanisms that underlie body

plans and thereby provide the potentials for further morphological change. To a certain extent, questions of mechanism reduce to ways in which characters are hierarchically correlated, in other words, the possibility that some characters are "preadaptive" for others. Saying that a character is preadaptive is essentially the same as saying that it is part of a body plan that constrains evolution along certain lines.

The general questions posed above can be made more specific with regard to primates. First, is the order Primates characterized by a single body plan and set of constraints that distinguishes that order from other mammals? Second, do subclades of primates exhibit particular body plans? Le Gros Clark's (1934) discussion of evolutionary trends in primates gives a strong impression of an overall primate body plan and the idea that initial characters gave rise to potentialities. Salient aspects of the primate body plan can arguably be summarized as follows: relatively large brain, grasping hands and feet, frontated and convergent orbits, and enhanced visual acuity. These aspects of the primate body plan are typically discussed in theories of primate origins, though opinions vary on which of these is most critical for the origin of primates (Cartmill, 1972, 1992; see also references in Fleagle, 1999). But is this description more than a summary of what traits are shared among primates alive today? From a developmental standpoint, Hall (1992) argued that features most integral to a body plan would be expected to be the least variable in the group described by the body plan. This sets up a way in which the hypothesis of a primate body plan can be tested.

One apparent problem with the concept of a primate body plan is that the two major suborders, Haplorhini and Strepsirhini, are qualitatively different in many respects, including the features listed above as characteristic of primates as a whole. Moreover, this criticism could be leveled at the hypothesis of a body plan that characterizes either suborder. Such a "problem" may, however, constitute evidence that body plans are actually "nested" at different levels in the phylogenetic hierarchy of primates. It is unclear at present whether the effects of body plans

on morphological evolution, i.e., the effects of morphological constraint, take place at certain levels more than others. This is an open question, and an important one that may be key to understanding why groups at many levels appear to express homoplasy in some features more than others.

Epigenesis

As shown above, definitions of homology and homoplasy are often discussed with respect to the developmental basis of adult form. Further issues with respect to development have to do with whether the timing of formation of a feature, or its response to epigenetic stimuli, generate predictions about homoplasy. For example, are features that appear late in development more prone to homoplasy? And are features with a strong epigenetic component less reliable as indicators of phylogeny?

These two questions are related to one another, because features that appear late in development and features that are responsive to stimuli, such as mechanical loading or metabolic rate, can be viewed as more superficial than other traits, or more distinct from the genome. The theoretical basis for favoring early-developing, "preformed," or more canalized traits in a phylogenetic analysis is the idea that they have a stronger genetic basis, i.e., they are more heritable.

The requirement for application of this philosophy is either knowledge of early developmental stages, such as the occurrence of several adult Neandertal traits in infant Neandertals (Tillier, 1989; Rak et al., 1994) or knowledge of how activities or environmental conditions during ontogeny affect traits in adults (Lieberman, 1992, 1996). However, even when such information is available, the relative phylogenetic information content of these traits versus other traits has not been addressed explicitly in a phylogenetic framework.

Nonetheless, some indirect inferences can be drawn based on comparisons of how different anatomical systems behave. For example, most dental traits used in phylogenetic analyses describe teeth before they are exposed to external epigenetic forces. One would predict, based on this information

alone, that dental traits would be better predictors of phylogeny than other anatomical systems such as the skull, which is highly epigenetic in form (see reviews by Lieberman, 1992; Herring, 1993). Studies by Sanchez-Villagra and Williams (1998) and Ross et al. (1998) have compared homoplasy in dental traits to other types of morphological data, the former in a broad-based comparison across mammalian groups, and the latter in a detailed study of anthropoid relationships. Neither study favored the view that dental traits show less homoplasy, and Ross et al. (1998) leaned toward the conclusion that dental traits may be *more* prone to homoplasy. In other areas, phylogenies based on dental data have generally not been verified using other anatomical systems, including genetic traits. For example, the phylogeny of Kay (1990) for New World monkeys was based entirely on dental traits and is inconsistent with some congruent aspects of other parsimony-based studies of this group (e.g., Ford, 1986; Schneider et al., 1996; Horovitz and Meyer, 1997).

In the case of dental traits, which do occur early in development, there is the complicating factor that they are also regarded as highly adaptive and responsive to selection, which may suggest an increased tendency to homoplasy (but see the section on "Adaptation" below). Nonetheless, no empirical study has demonstrated that traits arising early in development are less prone to homoplasy. It is therefore useful to reexamine the theoretical basis for this expectation.

Developmental trajectory and plasticity can be selected for, just as are adult phenotypes (Schlichting and Pigliucci, 1998). Traits that appear late in a developmental sequence are presumably not selected to occur at earlier developmental stages. In sexually dimorphic species where males are larger, dimorphism is usually not expressed in juveniles. This is because the basis for dimorphism, sexual selection, is not operating on juveniles.

Other traits that occur late in development may not seem to serve a clear function on their own, but instead are responses to various epigenetic processes. Sagittal crests, or any pattern of crests on the vault, are for the most part a response to the orientation

and action of cranial musculature. The formation of these crests usually occurs late in development and has a similar mechanism in many different mammalian taxa. Lieberman (1999, p. 148) regarded the ubiquity of mechanisms such as this as a problem, because given a widespread shared mechanism, "phylogenetically irrelevant stimuli can elicit similar morphological responses" (= homoiology, parallelism). Thus, this is an example of a trait that would probably be given less weight in a scheme that emphasizes features that occur early in development or are canalized.

On the other hand, a trait such as a sagittal crest serves as a skeletal proxy for many characters that are usually not included in character lists of fossils, such as those having to do with muscular development and orientation. Because of this extra information, and potential complexity of form, the configuration of crests on the vault can potentially be viewed as a valuable character in studies of phylogeny.

Development, or epigenesis, is clearly fundamental to the study of homoplasy because it describes how form is generated, and homoplasy, ultimately, represents a statement of how form relates to ancestry. Recent trends to integrate developmental and evolutionary biology provide welcome insight into the processes that underlie homoplasy or homology (Hall, 1992, 1998; Wray, 1994; Shubin et al., 1997; Lieberman, 1999; McCollum, 1999). However, it is clear that different theoretical approaches can be used to develop contradictory expectations about how knowledge of development will allow us to discriminate between phylogenetically informative traits and those that are prone to homoplasy. As with many of the topics discussed in this paper, empirical studies are needed to test these hypotheses.

Allometry

The study of allometry provides detailed examples of functional and structural constraints in primate evolution, as it has been studied in a wide variety of groups and applied to many different characters. There are three kinds of allometric relationships: interspecific (evolutionary), intraspecific (static), and ontogenetic (Fleagle, 1985;

Schlichting and Pigliucci, 1998). With respect to phylogenetic analysis, the finding of an interspecific allometric relationship can have the same effect as evidence of adaptation. It provides a useful explanation for the presence of a certain feature, but at the same time calls into question the utility of that feature for resolving phylogenetic relationships. For example, Ford (1994, p. 598), in refining an earlier character list of anthropoid postcranial traits, noted that "...those [characters] that were clearly primarily the result of size differences (allometry) were excluded." Allometric characters are excluded from phylogenetic analyses for two primary reasons: they may represent suites of correlated traits, all tied into a common factor of size, or they may be particularly prone to homoplasy, as size itself is widely considered to be. Our interest in allometry in this review stems from its importance as a constraint that leads to similarities in taxa across many different lineages, but also the recognition that allometric patterns describe particular monophyletic groups, whether these are groups of individuals within species, or groups of species within higher clades.

Allometry can be described as a structural constraint in general, i.e., the constraint of size on morphological shape; a functional constraint, if size and a particular trait become coupled in a fixed way in the evolution of a group; and/or a developmental constraint, in the case of ontogenetic allometries. Rensch (1959) and Hennig (1966) both viewed allometry as a primary source of parallelism or homoiology, i.e., homoplastic traits with the same underlying basis. Gould and Lewontin (1979) considered allometry to be one of many possible "nonadaptive" explanations for morphology. Grehan and Ainsworth (1985, p. 184), in their discussion of different concepts of orthogenesis, stated that "We believe that allometry should be recognized as an expression of internally directed change and, therefore, is orthogenetic." The common theme is that homoplastic traits due to allometry probably reflect a homologous process at a lower level.

Allometric changes represent intrinsic factors in the sense that they are expressed in relation to organismal size. Nonetheless, the

allometric relationship on the whole can be argued to be adaptive, since it enables maintenance of functional equivalence across a size range. For example, Jungers' (1979) study of limb proportions in lemurids and indriids found different interspecific allometric trajectories within each family. He argued that the trajectories themselves were adaptations to particular locomotor behaviors. Indriids emphasize vertical clinging and leaping to varying degrees, and in order to maintain this ability, large-bodied forms seem to have relatively long forelimbs and short hindlimbs. This pattern results because, relative to trunk length, hindlimb length is isometric in indriids, while forelimb length is strongly positively allometric. In this case, as in many others, the expression of an allometric trait is ultimately related to the environment and selective regime of a particular behavior. "Intrinsic" and "extrinsic" factors are inseparable in this situation. Furthermore, entire trait-behavior complexes, such as suspensory behavior and a host of morphological traits in primates, are often argued to be allometric (e.g., Fig. 5, and Fleagle, 1985, 1999).

It is routine to attribute allometric relationships to particular groups in a wide variety of contexts and at many levels in the taxonomic hierarchy, from genera to orders (e.g., Jungers, 1979; Martin, 1990; McHenry, 1991; Ravosa 1996a,b). As with body plans, allometric relationships can be argued to be "nested" within each other. The level at which groups differ depends on the level of the study. Within vertebrates, mammals exhibit a characteristic relationship of brain to body size, and within mammals, carnivores, insectivores, and primates all exhibit distinctive relationships (Martin, 1990). Moreover, the nested, or hierarchical, nature of allometries extends down below the species level. Static allometric relationships within adults of a species are often different from those among species in a closely related group (Cheverud, 1982).

Given this combination of constraint and group specificity, what does allometry mean for homoplasy? When allometric traits evolve in parallel, we would expect them to do so in characteristic ways for particular groups. This almost certainly means that different

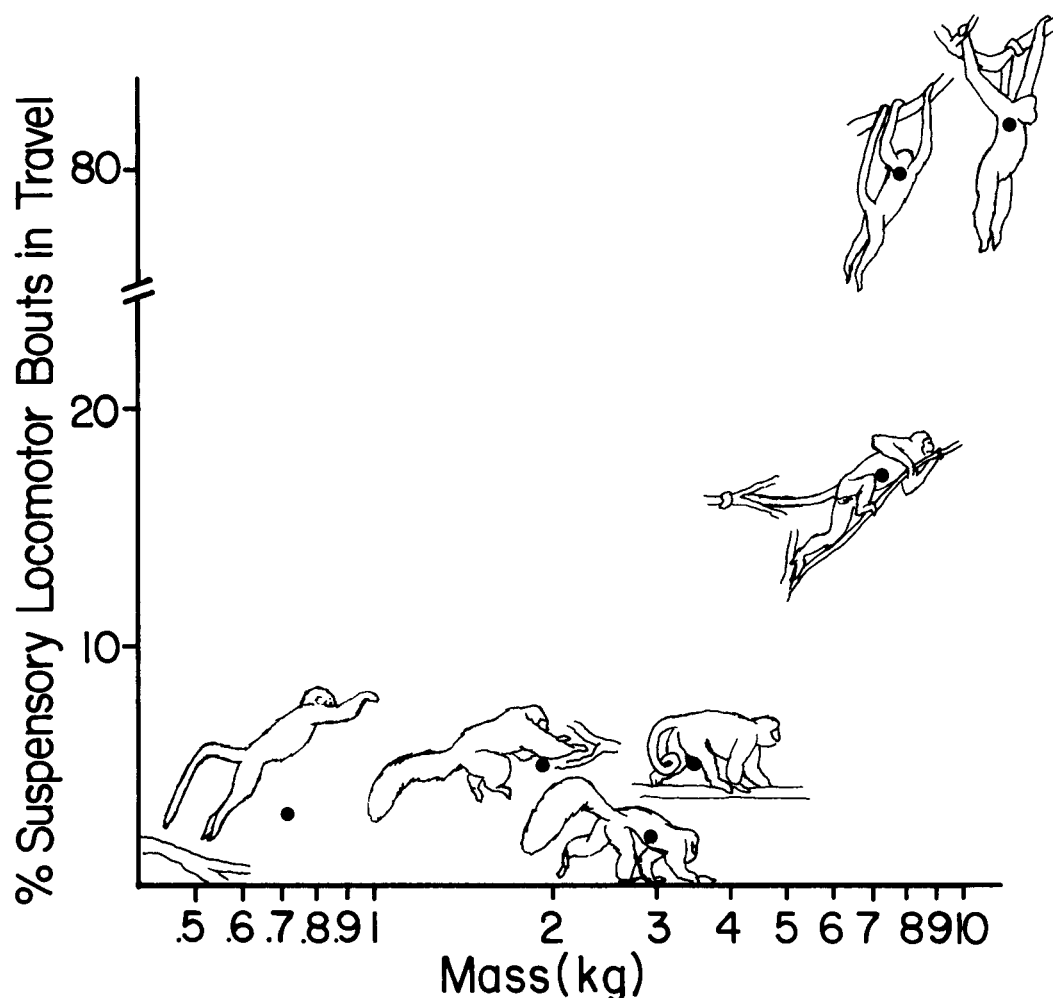


Fig. 5. Allometry of locomotor behavior. Large-bodied primates show lower frequencies of leaping and higher frequencies of suspension. From Fleagle (1999).

groups should exhibit homoplasy in different traits.

When patterns of allometry are identified for particular groups, it is usually because these groups are defined by prior phylogenetic or taxonomic analysis. Allometric information has been underutilized, so far, to *inform* the selection of phylogenetic hypotheses. Patterns of ontogenetic or other intraspecific allometries can theoretically be used as characters, because in this case there is a valid unit of analysis, the species, defined by methods independent of the allometric analysis. In some cases, such as among African

ape crania (Shea, 1983, 1985), ontogenetic allometries may be the same among closely related species and can serve as characters. At a higher taxonomic rank, it is possible that similar patterns of allometry *within* two or more well-defined families may provide some indication of a relationship *between* families. Thus, allometry is at one level a source of phylogenetically misleading parallelism, but at another level, it is potentially informative about underlying processes shared among related organisms. For example, see Leutenegger's demonstration that litter mass scales differently in haplo-

rhines and strepsirrhines. This situation epitomizes the need to distinguish levels of analysis, as discussed above.

We dwell on allometry because it appears to be the most well-known area of study in primates that serves to link characters to the constraints that govern their expression. Multiple species evolving larger body size within a clade that has a characteristic allometric pattern will appear to undergo dramatic parallel evolution. At the same time, allometric traits should not be quickly dismissed as phylogenetically uninformative. The relationship among them, or the nature of their relationship to size, may be characteristic of certain clades and therefore potentially informative about phylogeny.

Adaptation

Homoplasy is widely used to test hypotheses of adaptation. It is viewed by many as a critical aspect of adaptive explanations, because the repetition of events gives greater degrees of freedom to any analysis of association. The current trend is to incorporate phylogeny explicitly into these analyses (e.g., Harvey and Pagel, 1991; Brooks and McClenan, 1991; Larson and Losos, 1996; Purvis and Webster, 1999), but the general use of homoplastic similarity to suggest adaptation is common (e.g., Jolly, 1970; Cartmill, 1972; Jungers, 1977; Kay and Cartmill, 1977; Kay and Hylander, 1978; Godfrey, 1988; Fleagle and Anapol, 1992).

Although many definitions are in use, we consider a trait to be an adaptation for a function if it enhances the performance of that function and was selected to serve that function. Although this is what we believe is implied by use of the word adaptation, we acknowledge that methods of establishing adaptations are often inferential and assume, rather than demonstrate, natural selection as the predominant mode of occurrence of adaptations (see chapters in Rose and Lauder, 1996). There is considerable debate over the information needed to identify morphological or behavioral features as adaptations (Rose and Lauder, 1996; Ross, 1999) and trenchant disagreement over the roles of homology and homoplasy in identify-

ing adaptations (see Coddington, 1994; Wenzel and Carpenter, 1994).

No matter how adaptation is defined, hypotheses of adaptation always rely to some extent on the association of a trait with a specified function. Some suggest the relatively strict requirement that in all observable taxa that have the trait, the trait should enhance the same function (Kay and Cartmill, 1977). Others would only seek a statistically significant association. In either case, a strong association does not require that the trait originated more than once. Perfect association can result from a trait originating once in a common ancestor and being retained in all descendant taxa. The principal benefit of using homoplasy in studies of adaptation is that multiple origins of both trait and function *are* required, and these origins are themselves subjected to a test of association. These occurrences have greater independence from one another than does the presence of a trait in two closely related organisms who inherited that trait from a common ancestor (Harvey and Purvis, 1992).

For homoplastic traits, quantitative methods exist for analyzing the association of discrete traits or continuous traits in a phylogenetic context (e.g., Maddison, 1990; Harvey and Purvis, 1992; Purvis and Rambaut, 1995; Lindenfors and Tullberg, 1998). However, when quantifying the relationship of homoplastic characters, one must be careful not simply to equate correlation (with or without phylogenetic context) with adaptation (Coddington, 1994; Baum and Larson, 1991; Larson and Losos, 1996). While a principal benefit of using homoplasy to study adaptation is the opportunity to give statistical weight to trends, there must still be functional evidence to justify the hypothesis of adaptation. Association is only one criterion of adaptation.

This "homoplasy approach" to testing hypotheses of adaptation can be contrasted with the "homology approach" of focusing on single, unique changes in great detail (Eggleton and Vane-Wright, 1994, and references therein). As mentioned above, unique changes may produce perfect associations in descendant taxa, but these associations rep-

resent only a single origination. This difficulty has led to the more widespread acceptance of the homoplasy approach by students of primate and human evolution. For example, in reference to human adaptations, Cartmill (1990, p. 189) has concluded that "if there are qualitative human uniquenesses that find no analogies [= homoplastic similarity] of any sort among other species, they are not explicable." Despite the apparent weakness of focusing on single events, others have argued that they are sometimes preferred because more lines of evidence are usually brought to bear, including detailed knowledge of function, performance, and/or behavior (Coddington, 1994; Wenzel and Carpenter, 1994).

In anthropology, it is most often the case that a few homoplastic occurrences of a particular trait are combined with relatively detailed knowledge of the trait-function relationship in each group. Association is critical but not tested statistically because the number of events is small. An example of this approach is the recognition that many postcranial traits, particularly those of the trunk and forelimb, are homoplastic adaptations to forelimb-dominated suspensory behavior during locomotion in hominoids (possibly multiple lineages) and ateline New World monkeys (Rose, 1983, 1988, 1997; Sarmiento, 1987; Ward, 1997; Larson, 1998). Among extant primates, where positional behavior can be observed, and experimental studies of muscle function performed, these features represent two origination events, or three depending on the interpretation of hominoid evolution. The adaptive relationship between trait and function in atelines and hominoids is sometimes extended to make inferences about behavior in some fossil primates, whether they are members of these clades or not.

The support for this hypothesis of adaptation is strong not because of the number of events, which is low and cannot suffice for a statistical test of association, but instead because of the corroborative evidence from behavioral observations, experimental analyses, and arguments from design. In fact, the detailed and essentially complete picture offered by this example is perhaps more convincing than many arguments of adapta-

tion based principally on statistical association across large numbers of taxa.

This example brings up another issue, namely, the false dichotomy between adaptation and phylogeny that sometimes features in discussions of homoplasy: Homologous traits indicate phylogeny, whereas homoplastic traits indicate adaptation. The dichotomy is false because homologous, or uniquely occurring, traits can be adaptive, and homoplastic traits may reflect some process other than adaptation. Moreover, the relativity of these definitions becomes important: Some traits that appear to occur once within the in-group may be homoplastic at a more general level, and some traits that are homoplastic at a general level may still be informative at lower levels.

A dichotomy between phylogeny and adaptation also reflects deeply held suspicions that "adaptive," or ecologically driven, characters should be prone to homoplasy (e.g., Darwin, 1859; Eldredge and Cracraft, 1980). In anthropology, the adaptive significance of some features has led authors to suggest that whole complexes be downplayed in phylogenetic analyses (e.g., the hominin masticatory apparatus, Skelton and McHenry, 1992) or particular traits be dismissed from phylogenetic analyses because of their functional role (e.g., the fused mandibular symphysis, Ravosa and Hylander, 1994). Yet at the same time, phylogenetic analyses of primates typically have long lists of traits that seem likely to have some adaptive meaning. Most of these are not singled out for functional study, and, lacking evidence of function, they are retained in the analysis. This has the interesting result that the more we are able to explain the origin and function of a character or character complex, the less likely we are to use it for phylogenetic studies.

We caution against general application of this kind of logic. It is not possible in the study of primate evolution to parcel traits into categories such as phylogenetic or adaptive. Rather it is the interaction of the two areas of study that is of interest. Certainly there are cases where particular sets of characters provide a misleading phylogenetic signal, because they reflect adaptations to a certain behavioral regime, but

these situations are usually detectable and explicable with reference to other lines of evidence (e.g., Lockwood, 1999). Along the same lines, sets of data that appear to exhibit great amounts of homoplasy in one circumstance are unlikely to show such a pattern *generally*. For example, fusion of the mandibular symphysis is widely homoplastic within strepsirhines, but serves as a distinct synapomorphy of anthropoids. And in hominoids, some suspect that suspensory adaptations may be homoplastic in gibbons and other modern hominoids (Rose, 1997), but others see the same traits as informative with regard to the phylogenetic position of *Oreopithecus* (Harrison and Rook, 1997).

In summary, homoplasy often plays a critical role in the study of adaptation because it provides multiple "natural experiments" of morphological features associated with behavioral or ecological features. However, homoplastic patterns cannot (by definition) be used to explain traits that have evolved uniquely, and in many cases these features are the most intriguing examples of adaptation (Coddington, 1994; Wenzel and Carpenter, 1994). Finally, it is unclear that there is reason to use evidence of adaptive homoplasy in one clade to expect homoplasy in the same traits in another clade or ecological context.

Behavioral ecology

There have been relatively few attempts to examine the phylogenetic patterns exhibited by features of behavior and ecology among primates, despite strong opinions held by many anthropologists on this topic. Most primatologists seem to feel that features of behavior and ecology, such as social group size, patterns of interindividual interactions, infant care, as well as diet and locomotion exhibit considerable homoplasy within primates. The predominant paradigm in primate behavioral ecology during the past four decades has been socioecology, which seeks to relate differences in social behavior to patterns of resource distributions in the environment (e.g., Jay, 1968; Janson, 1992; Lee, 1999). Most studies rely on correlations between behavior and ecology in extensive homoplastic interspecific comparisons (e.g., Clutton Brock and Har-

vey, 1977; Janson and Goldsmith, 1995; Wrangham et al., 1993). Indeed, many primatologists would probably openly question whether it is either feasible or appropriate to examine behavior and ecology in a phylogenetic context for several reasons: (1) Many aspects of behavior and ecology are subject to well-documented intraspecific variation; (2) homology can be very difficult to assess for behavioral characters (e.g. Robson-Brown, 1999); and (3) behavior may change throughout an individual's lifetime, often as a result of local environmental conditions.

However, as several reviewers have emphasized (e.g., Rendall and Di Fiore, 1995; Greene, 1994, 1999; Procter, 1996; Foster et al., 1996), most of the "problems" that may make behavioral features unsuitable for phylogenetic studies are to some extent equally true for morphological features. Indeed, the few studies to compare amounts of homoplasy in behavioral and morphological features have found no evidence that behavioral features are more subject to homoplasy than are morphological features (de Queiroz and Wimberger, 1993; Prum, 1990; McLennan et al., 1988; Miller and Wenzel, 1995; reviewed in Procter, 1996). No such formal comparisons have yet been made for primates, but there is no doubt that, as discussed above, the choice of characters, whether molecular, morphological, or behavioral, that are used in any analysis can have a profound effect on levels of homoplasy. At this point, primatologists should keep an open mind about levels of homoplasy in primate behavior and ecology.

Despite some skepticism about the utility of phylogenetics for understanding behavioral ecology, there have been attempts to examine primate behavior and ecology in a phylogenetic context since the beginning of the discipline (e.g., DeVore, 1963) and studies of socioecology have clearly recognized strong phylogenetic patterns in primate behavior and ecology (Crook and Gartlan, 1969; Struhsaker, 1969; Spuhler et al., 1975; Wrangham, 1980, 1982). More recently, studies of primate behavior and ecology have begun to incorporate phylogeny from two different perspectives (Fleagle, 1992; Rendall and Di Fiore, 1995). Comparative studies of primate adaptation, which are meant

to examine homoplastic changes in independent lineages (see section on adaptation above), increasingly incorporate formal analytical methods that attempt to "correct" for correlation among related taxa that artificially inflates the statistical significance of correlations or associations (e.g., Cheverud et al., 1986; Harvey and Pagel, 1991; Rendall and DiFiori, 1995; Smith, 1994; Nunn, 1995; Purvis and Rambaut, 1994). Indeed, this problem was identified by Darwin in *The Origin of Species* (1859). For example, Sillen-Tullberg (1993) used phylogenetic methods to examine the relationship between mating systems and visual signals of ovulation among primates. Although students of primate behavioral ecology have used these "corrections" less than those of other vertebrates, the use of phylogenetic methods in comparative studies is becoming increasingly common in primatology (see Lee, 1999).

In addition to studies which have attempted to incorporate formal assessments of homoplasy into comparative analysis, several authors have directly examined the phylogenetic patterns in aspects of primate behavior and ecology to identify homologous and homoplastic features. Wrangham (1987) and Ghiglieri (1987) have examined the evolution of social behavior among great apes. Each researcher identified a suite of features that were characteristic of the last common ancestor of the great ape-human clade. Kappeler (1998–1999) has examined nesting behavior and broad aspects of primate social systems in a phylogenetic context. In each of these cases, the researchers mapped features of behavior and ecology onto a primate phylogeny (e.g., Purvis, 1995) to determine which features are homologous and which are homoplastic.

In the most comprehensive study of primate behavior and phylogeny to date, Di Fiore and Rendall (1994; also Rendall and Di Fiore, 1995) examined the distribution of 34 behavioral traits (including dispersal patterns, grouping patterns, social and sexual relations, and parental investment) in 65 species from 37 genera of primates. Di Fiore and Rendall (1994) performed two separate analyses. First, they used the behavioral features to generate a most parsimonious

tree for primate genera. This most parsimonious tree was very different from any conventional primate phylogeny based on morphological or molecular studies (e.g., Purvis, 1995; Fleagle, 1999), indicating that the behavioral features are indeed quite homoplastic among primates. For example, monogamous species from many separate groups of primates grouped together in a clade using their behavioral features. Living apes did not group together, but scattered widely among other primates — *Pan* grouped with *Ateles*, *Gorilla* was a sister group to cercopithecoids, and *Pongo* by itself. However, behavioral variables group most living cercopithecoid monkeys into a single clade on the basis of numerous shared features.

Next, Di Fiore and Rendall (1994) examined how their data mapped onto a traditional phylogeny of primates. In this approach, the clade of cercopithecoids was characterized by a suite of derived features as were the cercopithecines. Other "natural" groups could also be characterized by a smaller number of shared derived features of social organization. For example, in their analysis, the clade of great apes and humans is characterized by tolerant females and male-dominated intergroup encounters. The consistency index (CI) for the behavioral data used by Di Fiore and Rendall was 0.61 when mapped onto a well-supported primate phylogeny. Thus, the homoplasy index (HI) is 0.39, which compares favorably to the HIs from morphological data sets in primates, once the number of taxa is taken into account (Table 1).

Homoplasy in primate behavior and ecology has also been examined by several other researchers in the context of community similarities and differences. Fleagle and Reed (1996) showed that in quantitative features of behavior and ecology there was considerable overlap, and hence homoplasy, among individual species of different geographical regions. Similarly, in analyses of the relationship between ecological distance and phylogenetic distance, Jernvall and Wright (1998) and Fleagle and Reed (1999) showed that there is both divergence and convergence in the ecological attributes of distantly related taxa; the convergence primarily reflects homoplasy.

More generally, simple mapping of behavior and ecology on accepted phylogenies can yield important insights into the patterns of behavioral evolution (e.g., Wrangham, 1987; Ghiglieri, 1987; DiFiori and Rendall, 1994; Rendall and DiFiori, 1996). Only by examining behavior and ecology in a phylogenetic perspective can we understand the evolution of individual features and determine how extensive homoplasy actually is and if some features of behavior and ecology are more susceptible to homoplasy than others.

Generality of explanations

The sections above highlight many potential explanations for homoplasy, many of which are not mutually exclusive. Before proceeding with some detailed examples, we should emphasize the importance of determining the applicability of these explanations, in other words, the generality of answers to questions such as the following: Is this character phylogenetically informative? Is allometry the explanation for homoplasy in this character and group? Are behavioral traits labile in evolution and prone to homoplasy? Are "adaptive" characters more prone to homoplasy?

There is a sentiment that characters should be generally homoplastic or not, regardless of the group being studied. In primates such as hominoids (Rose, 1997), adapids (Godinot, 1998), strepsirhines (Ravosa and Hylander, 1994), or hominins (Skelton and McHenry, 1992; McCollum, 1999), researchers have questioned the utility of some traits for determining phylogeny in one clade because they are homoplastic in another. Pilbeam (1997, p. 17), following Sarich (1993), has expressed the view that if "the unbounded nature of morphological data means that a character useful in one situation is not necessarily useful in another, we are in trouble." If anything, the evidence provided by examples discussed below and throughout this paper suggests that characters are *not* uniformly either homoplastic or phylogenetically informative, and that explanations for homoplasy vary between groups. This does not necessarily mean "we are in trouble," but it may mean that the phylogenetic solution to homoplasy is not simply to obtain a list of characters that are always

informative about relationships and then to restrict analysis only to those characters.

EXAMPLES

Having discussed many of the issues involved with biological sources of homoplasy, we present several extended examples to demonstrate how these factors relate to one another and the ways in which certain patterns can be informative. These examples are focused on specific characters and functional complexes (e.g., brain morphology, symphyseal fusion of the mandible) or particular groups (papionins, platyrrhines, early hominins, and modern humans).

Brain size and sulcal patterns

Brain sizes are relatively well known in modern primates. Inferences regarding possible trends in primates require information on fossil primates. While difficult to obtain, estimates for relative cranial capacity in fossil primates are generally found to be less than those for their close relatives among modern primates (Martin, 1990). Thus, increases in brain size appear to be common (and homoplastic). This may represent a trend resulting from some kind of intrinsic benefit, and evidence also exists for increases in brain size in other mammalian groups during the Tertiary period (Jerison, 1973). Still, the lack of good brain and body size estimates for fossil taxa makes it difficult to test these ideas rigorously in a phylogenetic framework.

Something that is more clear in primates, and mammals as a whole, is that the complexity of sulcal patterns on the brain depends directly on absolute brain size (Fig. 6) (see review by Hofman, 1989). Because gray matter, housing the nerve cell bodies, is distributed around the surface area of the brain, and white matter occupies the central part of the brain, an important scaling relationship is created between the convolutions of the brain surface and the total volume of the brain. If the brain's surface area remained perfectly smooth, the surface area relative to brain volume would reduce with larger brain size. However, it has been observed that surface area nearly keeps pace with increasing volume. Hofman (1989) found that the total cortical surface area of

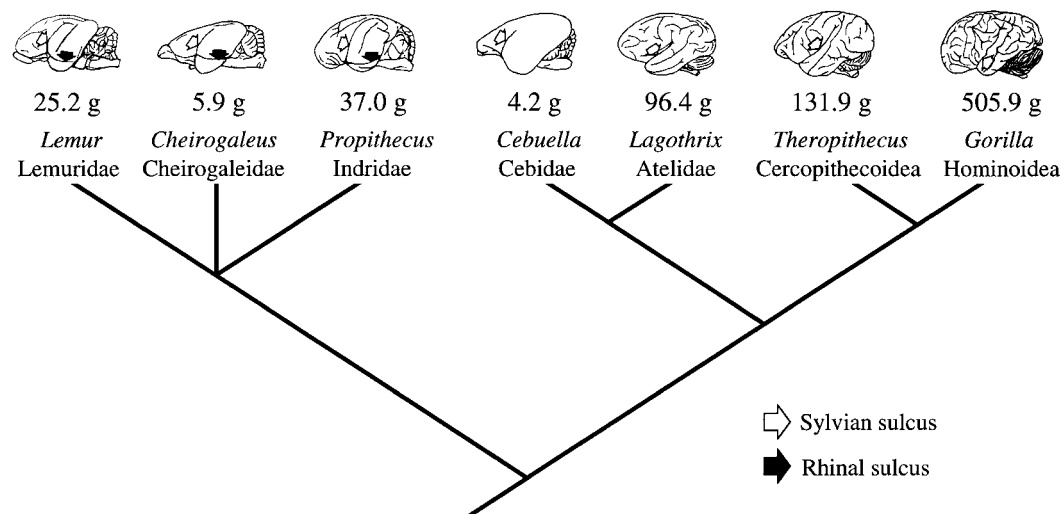


Fig. 6. Relationship between brain size (represented by mass), cortical folding, and phylogeny. Outline drawings from Martin (1990); brain masses are from Harvey and Clutton-Brock (1985). The phylogenetic relationship is schematic in order to show the relative positions of the taxa displayed. Selected taxa are not intended to

be representative of their families, but instead show a range of size and morphology. The Sylvian and rhinal sulcus appear to be phylogenetically informative traits, but the presence or absence of other sulci is strongly dependent on brain size.

mammalian brains scales to total brain volume with a coefficient of 0.90 on a logarithmic scale. This represents positive allometry of brain surface area, as the brain changes the shape of its surface in order to maintain functional equivalence in the proportion of gray to white matter.

Nested within this general plan for the mammalian brain are group-specific patterns. Zilles et al. (1989) used a gyrification index to express degrees of convolution in surface area. Measured from cross sections, the index is the length of the complete contour of the surface area divided by the length of the outer contour alone. The expectation is that the gyrification index should increase with larger brain sizes, and Zilles et al. (1989) confirm that this is the case for primates. However, what is most important about this study is the difference in regression lines between anthropoids and prosimians. The slope is 0.66 for anthropoids and 0.23 for prosimians, "indicating that for every unit increase in brain size, anthropoids acquire a higher degree of cortical folding than do prosimians" (Zilles et al., 1989, p. 146).

This example highlights two important aspects of homoplasy. On the one hand, the

underlying relationship between convolutions of the brain's surface area and total brain size gives rise to potential homoplasy, as parallel increases or reductions in brain size will usually occur with shifts in sulcal development. Zilles et al. (1989) note, for example, that the similar degrees of gyrification in callitrichids and prosimians represents convergent evolution as a side effect of small brain size. This relationship would presumably affect the use of individual sulci as phylogenetic characters. Diagnostic sulci of a particular group will not be present in members with small brains, and if small brains are the primitive condition, this situation could be especially confusing. In the terminology used above in definitions of homoplasy, the relationship between surface convolutions and brain size represents a structural or functional constraint on brain organization that governs the phenotypic expression of surface morphology.

The second important point is that the relationship of gyrification and brain size is group specific. The relationship itself can be considered as an "underlying synapomorphy" of a clade such as anthropoids, which means that apparent patterns of homoplasy — in expressions of particular sulci or

length of sulci — will be unique to anthropoids. Anthropoids are said to possess coronally oriented sulci, and strepsirhines rostrocaudally oriented sulci (Radinsky, 1970, 1974; Zilles et al., 1989; Martin, 1990). These sulcal patterns may be group specific, but they are only detectable above a certain brain size. This is a fairly clear example of a structural/functional constraint on character emergence. Certainly in this case it can be said that at some point a potential arises that is manifested when brain size is large enough.

In the anthropoid case, the relationship between gyrification and brain size is probably a derived condition, because the tarsier falls well within the strepsirhine cluster in plots of the gyrification index and brain size (Zilles et al., 1989). At the same time, the anthropoid condition exists within the general plan of the mammalian brain, illustrating very well the nested pattern of what might be called body plans, and the hierarchical nature of explanations of homoplasy.

Allometry and the mandibular symphysis

Another good example of homoplasy and its potential explanation is fusion of the mandibular symphysis in primates and other mammals. Ravosa and Hylander (1994, p. 464), citing Beecher (1977), have stated explicitly that “the likelihood of a fused symphysis as a result of functional convergence (i.e., homoplasy) makes symphyseal fusion a poor character for establishing phylogenetic affinities in any mammalian group.” This came as the conclusion of a review of relatively detailed evidence for the function of a fused symphysis and its allometric relationships.

According to Ravosa and Hylander (1994), the function of the fused symphysis is to resist wishboning stress and dorsoventral shear within the mandible and therefore allow increased recruitment of balancing-side muscle force. A fused symphysis is a synapomorphy of living anthropoids, regardless of how much homoplasy it shows in other groups, and has not undergone reversal within anthropoids. In strepsirhine primates, a fused or partially fused symphysis is homoplastic and appears to be closely related to jaw size (Fig. 7). Ravosa and

Hylander (1994) argue that the source of allometry in fusion of the strepsirhine mandibular symphysis is a combination of positive allometry of diet toughness and constraints on force production arising from the negative allometry of jaw muscle size with skull size (Scapino, 1981, Beecher, 1983). At some body size, this combination elicits partial or full fusion of the symphysis.

Ravosa and Hylander (1994, p. 464) add that “at the subordinal level in mammals, there is considerable body size variability at which adults develop a completely fused symphysis.” They suggest that the source of different allometric patterns may relate to differences in jaw-muscle recruitment patterns or to differences in the orientation of the jaw muscles. Moreover, some mammalian groups, such as carnivorans, may not exhibit an allometric basis for mandibular fusion at all (Scapino, 1981).

Thus, the presence or absence of a relationship between size and symphyseal fusion is probably group specific, and likewise is the pattern of this relationship. Saying that this allometric relationship is group specific implies a functional constraint determined by features related to the mandibular symphysis, in essence, aspects of the body plans of each of these different groups. Homoplasy in the evolution of a fused or partially fused mandibular symphysis would therefore be expected to show group-specific patterns as well. In strepsirhine primates, the pattern of homoplasy is dependent on allometry, while anthropoid primates show a noticeable lack of homoplasy in this feature. The latter may imply a strong phylogenetic constraint or irreversibility in this feature (Ravosa and Hylander, 1994; Ravosa, 1999).

Because of variability in how, why, and when fusion of the mandibular symphysis occurs in different groups, it is not clear to us that the character should be ruled out of phylogenetic analyses in a particular group without some evidentiary basis other than homoplasy in one or even several groups. But more importantly, the mandibular symphysis shows how an understanding of allometry and functional morphology can provide useful explanations of homoplasy. In this case, the homoplasy in strepsirhines might better be referred to as latent homology.

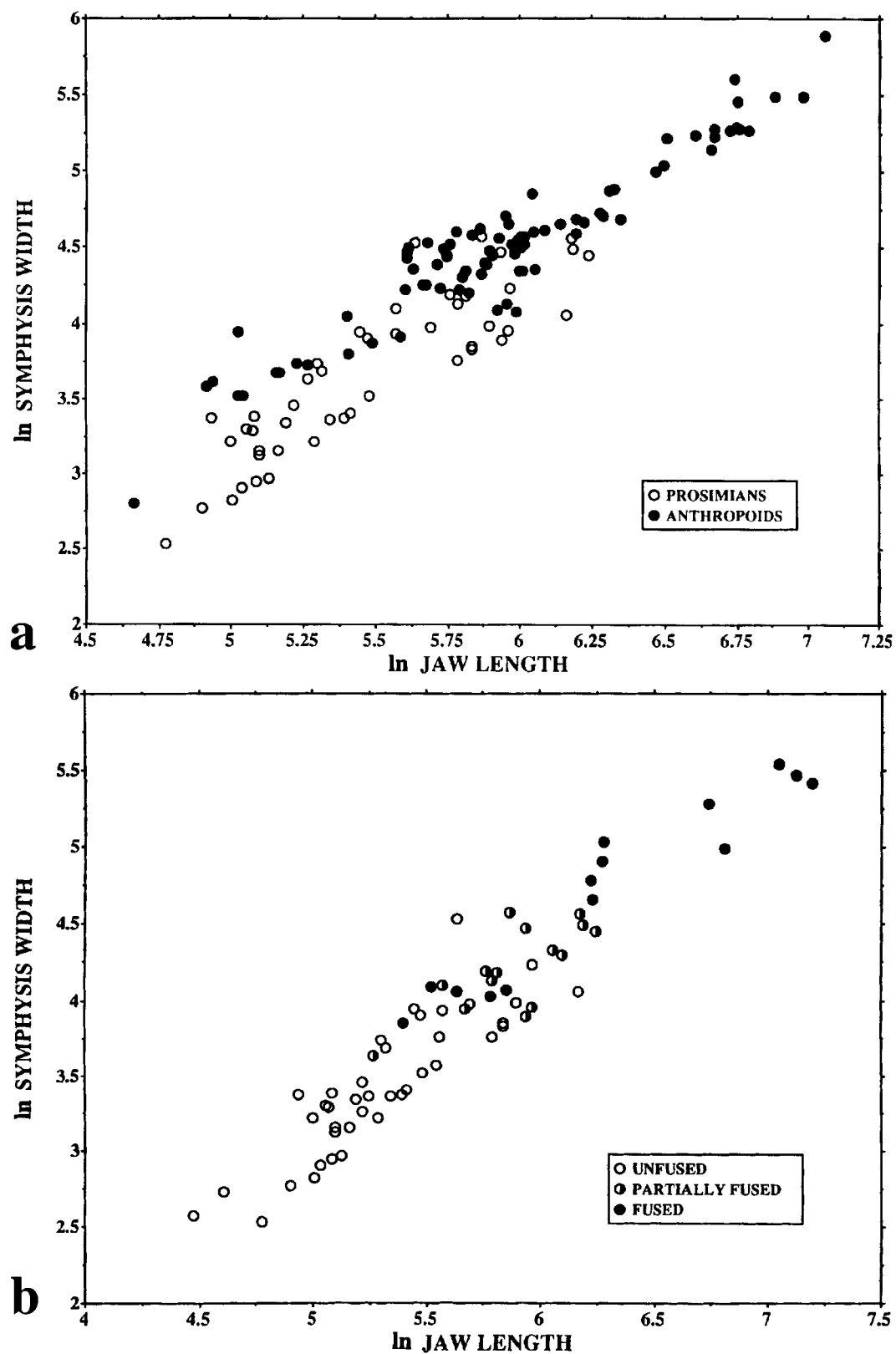


Fig. 7.

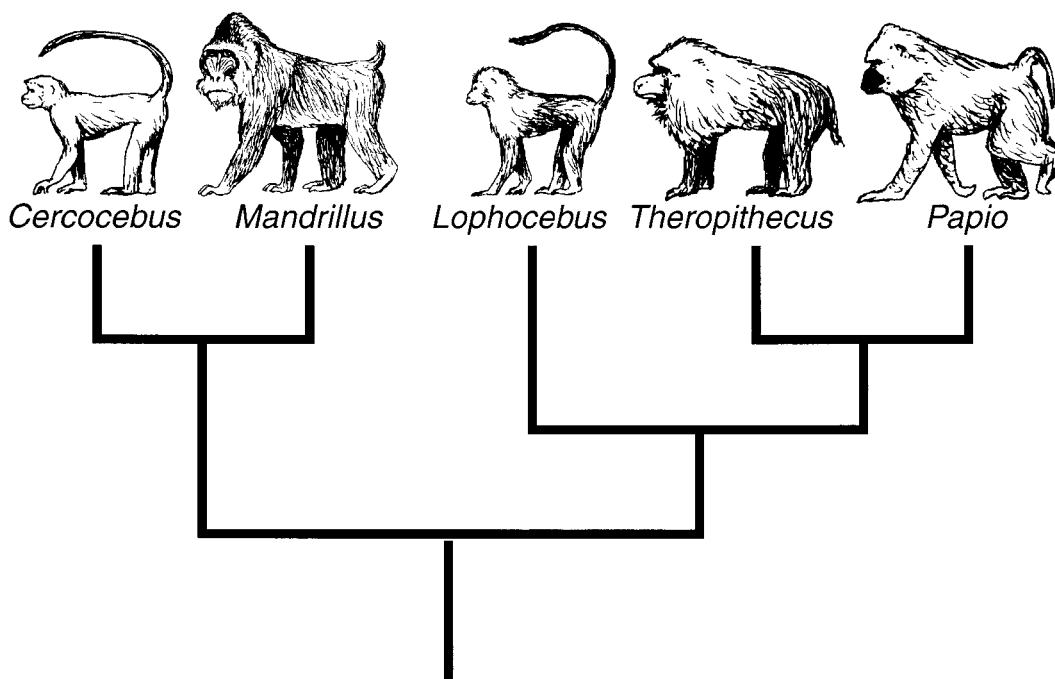


Fig. 8. Phylogeny of African papionins (Hewett-Emmett et al., 1976; Cronin and Sarich, 1976; Disotell, 1994; Harris et al., 1998). Prior to the incorporation of molecular data, the large-bodied taxa were regarded as a clade.

These primates probably share a generative process for symphyseal fusion that is related to allometry and jaw-muscle recruitment patterns, but the character is expressed only in certain members of the group.

African papionins

Large African cercopithecines have traditionally been placed into two seemingly natural groups — mangabeys and baboons (including mandrills). Many similarities of cranial and dental anatomy shared by mangabeys on the one hand, and by baboons and mandrills on the other, seem to support this grouping. However, numerous molecular studies from recent decades (Hewett-Emmett et al., 1976; Cronin and Sarich, 1976;

Disotell, 1994; Harris et al., 1998) have repeatedly demonstrated that mandrills are more closely related to one group of mangabeys, and baboons to another (Fig. 8). Moreover, many detailed features of skeletal and dental anatomy and a careful comparison of naturalistic behavior support the molecular phylogeny (Fleagle and McGraw, 1999). Clearly, there has been tremendous homoplasy in the evolution of mangabeys, baboons, and mandrills. The two mangabeys share distinctive features of the mandible and face as well as general characteristics, such as small size and long tails. Likewise, baboons, mandrills, and geladas share many cranial features, such as long snouts and jaws, and postcranial similarities, such as long limbs with skeletal adaptations for terrestrial locomotion, and high intermembral indices.

Some of the similarities among the smaller mangabeys and among the larger mandrills, baboons, and geladas in features such as snout length and limb proportions may be

Fig. 7. **a:** Relationship between symphysis width and jaw length in extant anthropoids and prosimians. The symphysis is fused in all extant anthropoids, and unfused in all extant prosimians. **b:** Relationship between symphysis width, jaw length, and symphyseal fusion in all prosimians, extant and fossil. Both figures are adapted from Ravosa and Hylander (1994).

allometric (and adaptive) similarities associated with size differences. Others may be simply retention of ancestral features. Regardless of whether the "mangabey" or "baboon" features are primitive, this radiation has generated remarkable amounts of homoplasy that has obscured the true phylogeny for several hundred years. Certainly, this is an example of homoplasy that deserves further study. Careful examination of developmental trajectories provides some insight into how the adult similarities have been achieved (Leigh, in preparation), and broad comparisons of fossil taxa and extant outgroups can help distinguish primitive and homoplastic similarities.

Hindlimb adaptations in atelid New World monkeys

New World monkeys, and specifically the atelines, have already figured prominently in some brief examples mentioned earlier in this paper, mainly for their development of suspensory behaviors and forelimb traits in parallel with some hominoids. We return to this group because atelines and pitheciines demonstrate parallelism in several hindlimb features probably related to climbing and hindlimb suspensory postures, as recently detailed by one of us (Lockwood, 1999).

Atelines and pitheciines are regarded as sister groups by most workers, and together these two subfamilies comprise the family Atelidae (Rosenberger, 1981, 1992; Ford, 1986; Schneider et al., 1993, 1996; Schneider and Rosenberger, 1996; Horovitz and Meyer, 1997; Horovitz, 1999). One phylogenetic question that is debated with respect to this family is the membership of pitheciines. What taxa are most basal in pitheciines affects interpretations of character evolution in atelids as a whole. If postcranially generalized taxa such as *Callicebus* and *Cebupithecia* are included in pitheciines, as recent analyses suggest (Horovitz and Meyer, 1997; Horovitz, 1999), then there are few if any postcranial synapomorphies of atelids. Instead, some postcranial characters arise in parallel in the two subfamilies within atelids. This is particularly true of hindlimb features, some of which are mapped onto a phylogenetic tree of platyrrhines in Figure

9, together with positional behaviors of extant taxa.

Characters such as the high femoral neck angle and reduced articular surface on the femoral neck allow increased mobility for climbing and hindlimb suspension and can be argued to be adaptations for these behaviors. Also, the evolution of these characters and positional behaviors as shown in Figure 9 is consistent with the hypothesis of adaptation, using the phylogenetic sense of adaptation as described by Baum and Larson (1991) and Larson and Losos (1996). Adaptation is an immediately obvious explanation for the homoplasy in these traits, but is it the only factor?

Allometry might also be expected to play a role, but these traits are drawn for the most part from a data set compiled by Ford (1994), who excluded character states thought to be primarily the result of allometry. Most pitheciines and atelines are larger than other platyrrhines, but *Cebus* is also relatively large-bodied and does not show all, or even most of the features illustrated in Figure 9. Although increased size is no doubt related to the evolution of suspensory postures and related morphological features in atelids, it does not appear to be the most proximate reason for the appearance of homoplasy.

Likewise, developmental constraints may limit the array of postcranial features likely to occur in platyrrhines, but the traits of interest here occur in other primates and even other mammals. Therefore, to the extent that constraints affect the expression of homoplasy, they are not specific to platyrrhines. This example, taken as a whole, illustrates the localized effects of adaptation in a particular group of primates. Because other South American mammals have evolved climbing and suspensory behaviors similar in some respects to atelids (e.g., White, 1993; Meldrum et al., 1997), Lockwood (1999) concluded that this pattern of homoplasy is primarily the result of extrinsic, ecological factors characteristic of South American forest structure, following on the hypothesis of Emmons and Gentry (1983) concerning prehensile tail evolution and suspension.

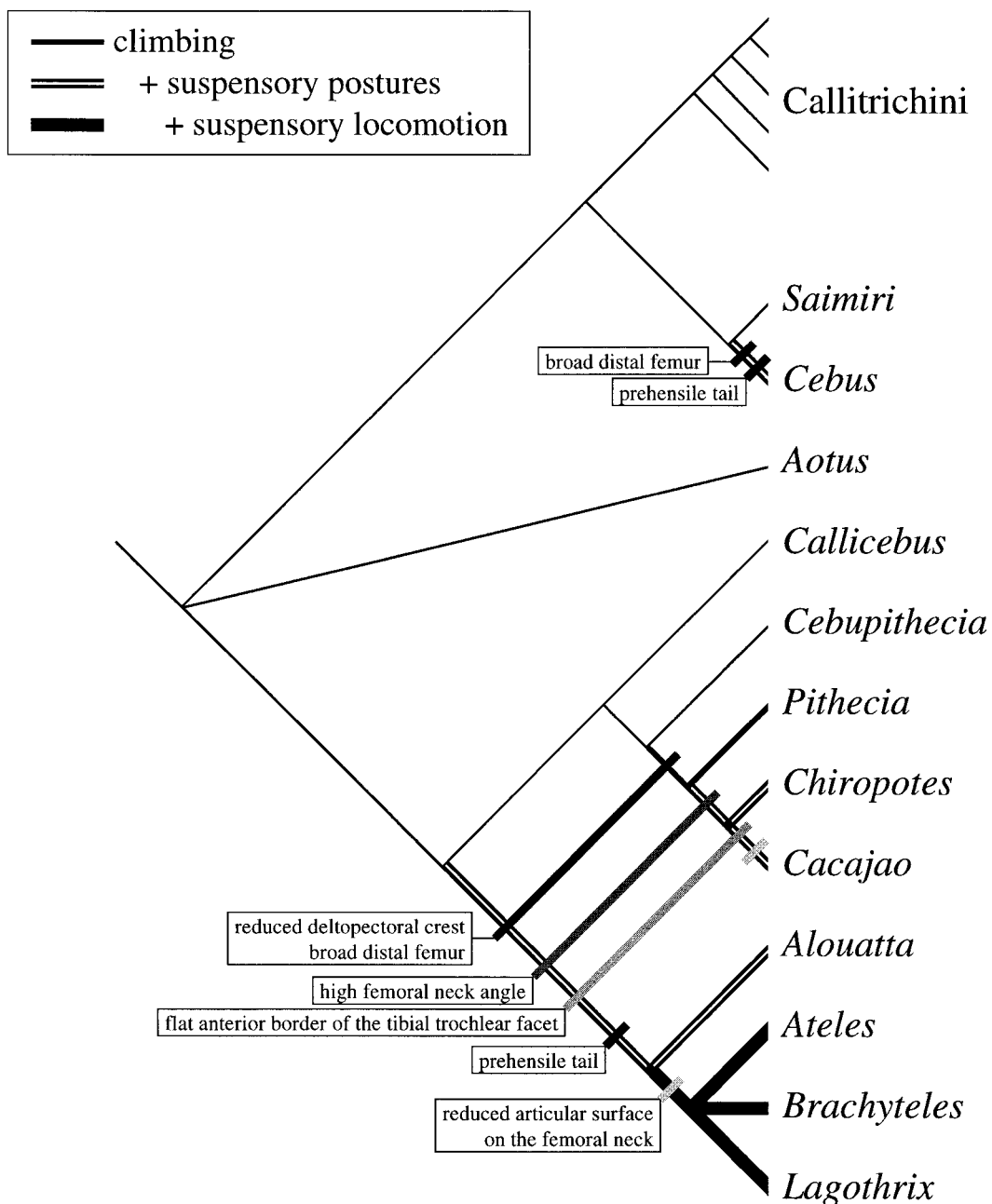


Fig. 9. Selected behavioral regimes and morphological traits mapped onto a phylogenetic tree of atelids (atelins and pitheciines) and other platyrrhines. From Lockwood (1999). All taxa are extant other than *Cebupithecia*. The behaviors indicated in the legend are addi-

tive, so, for example, atelins engage in climbing, suspensory postures, and suspensory locomotion. Homoplasy in the morphological traits is argued to have an adaptive basis as described in the text and by Lockwood (1999).

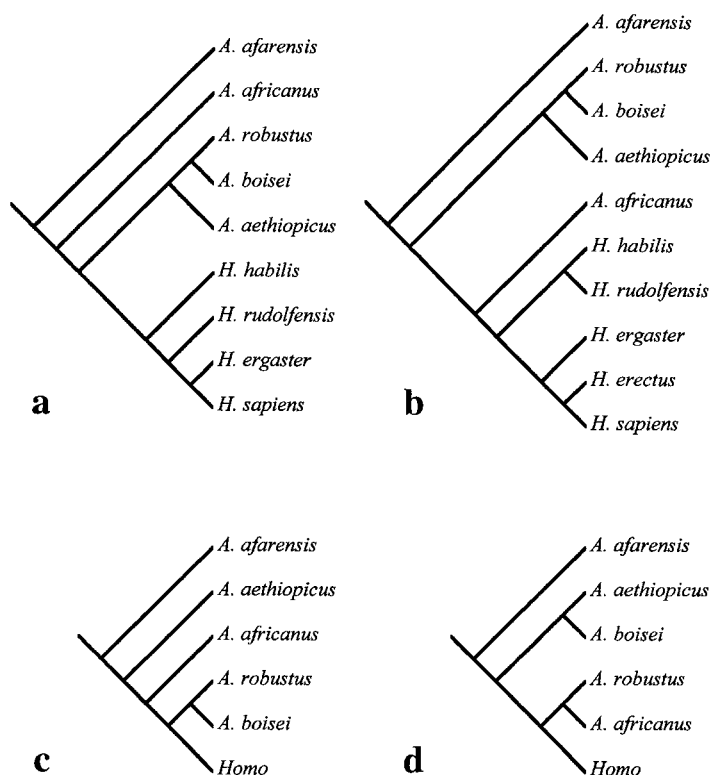


Fig. 10. Some alternative phylogenies of hominins that suggest different patterns of homoplasy. Those based on cladistic methodology are (a) Wood (1992), (b) Strait et al. (1997), and (c) Skelton and McHenry (1992). The last (d) is one of several alternative phylogenies that hypothesize separate origins of *A. robustus* and *A. boisei* in South and East Africa, respectively. These result from informal analyses of morphology not based on the principle of parsimony as usually applied (e.g., Walker et al., 1986; Kimbel et al., 1988; Kimbel, 1995).

The importance of homoplasy in these postcranial traits is not just that the pattern provides evidence of adaptation, but also that the homoplasy in some features goes unrecognized in analyses focused on postcranial traits (e.g., Ford, 1986). Thus, the homoplasy is patterned in a way that misleads the selection of phylogenetic tree and obscures the full extent of parallel evolution until other data sets are brought to bear on the same problem.

Early hominin phylogeny

There are few points of consensus about the phylogenetic relationships of early hominin species (Fig. 10). Most recent studies, and all of those that are cladistic in methodology, agree that *A. afarensis* is the sister group of a clade containing all later hominins (Kimbel et al., 1984, 1988; Skelton et al., 1986; Chamberlain and Wood, 1987; Wood, 1991, 1992; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997). In contrast, there is little agreement among these studies regarding such issues

as the monophyly or paraphyly of either the genus *Homo* or a clade containing *A. aethiopicus*, *A. robustus*, and *A. boisei* (see review by Wood and Collard, 1999).

Factors thought to play a role in these controversies center on homoplasy in craniodental traits. For example, some argue that the masticatory apparatus as a whole may be particularly responsive to selection because of its clear functional role, and thus lead astray phylogenetic analyses of the skull by linking species similar in diet but not in heritage (Skelton and McHenry, 1992). Other workers argue that homoplasy is no doubt common in hominin evolution, but that this reflects in part the inappropriate inclusion of poorly defined characters, characters that are strongly influenced by epigenetic factors (Lieberman, 1995; Lieberman et al., 1996), or the basic inadequacy of data from a single anatomical region such as the skull (Collard and Wood, 1998).

At the same time, different character lists for early hominins have made problems of character definition very clear (Lieberman

et al., 1996). Analyses such as those by Skelton and McHenry (1992) and Strait et al. (1997) take the same ranges of variation in several cases and parcel them into different numbers of traits. For example, Strait et al. (1997) described all of the following taxa as possessing a vertical tympanic plate: *A. aethiopicus*, *A. africanus*, *A. robustus*, *H. habilis*, *H. ergaster*, and *H. sapiens*. On the other hand, Skelton and McHenry (1992) used *three* different character states to describe variation in tympanic verticality among the same taxa. In addition, other studies, such as Chamberlain and Wood (1987), use characters that are entirely quantitative. Because of so many different approaches to character definition, it is easy to see how controversies can result. With each different phylogeny, a different pattern of homoplasy must be explained.

Perhaps the most prominent pattern of homoplasy in early hominins is that which is not present on any of the most parsimonious trees available. It is not uncommon for informal phylogenetic reconstructions to favor a hypothesis like that shown in Figure 10d, which accords with the parallel evolution of an *A. africanus*→*A. robustus* lineage in southern Africa and an *A. aethiopicus*→*A. boisei* lineage in eastern Africa, during the same time span (Walker et al., 1986; Kimbel et al., 1988; Kimbel, 1995). Researchers tend to reject this hypothesis on the grounds of parsimony because it implies dramatic amounts of apparent homoplasy (e.g., Wood, 1992; Strait et al., 1997).

There are several arguments that can be used to support such an unparsimonious phylogenetic hypothesis. The biogeographical and temporal distribution of taxa is concordant with this hypothesis, because with each of the putative lineages mentioned above, the primitive member comes earlier in time and in the same geographic region as the derived member to which it is most similar. Also, some consider many of the characters that conflict with this hypothesis to be subject to convergence because they are part of the masticatory apparatus and responsive to selection (Skelton and McHenry, 1992). In addition, McCollum (1999) hypothesizes that several of these traits are inextricably linked in develop-

ment and therefore not independent. The implication of the latter is that integrated trait complexes are easy to evolve. But as we discuss above, both of these hypotheses represent situations where traits that are relatively well-understood functionally and developmentally are downplayed in a phylogenetic analysis in favor of those traits about which we are more ignorant.

Thus, debates of early hominin phylogeny bring up issues of character definition and selection, the roles of functional morphology and development, and problems of how to integrate information on biogeography and stratigraphy with information from morphological data. As with other organisms, no phylogenetic hypothesis is free of homoplasy (McHenry, 1996). Favoring extrinsic sources of evidence leads to scenarios of more dramatic parallel evolution, but since the discovery of the Black Skull (Walker et al., 1986), any hypothesis of hominin phylogeny carries with it extensive patterns of parallelism and reversal (see Grine, 1988).

Modern human origins

Different concepts of evolution and methodological approaches to the question of modern human origins are starkly evident because researchers generally use the same type of data, but different methodology, to support contrasting hypotheses (Willermet and Clark, 1995; Lieberman, 1995; Smith and Harrold, 1997). Because of this, questions of character identification and definition are prominent. For example, Lieberman (1995) discussed character definition and selection, mainly with respect to issues of modern human origins. He gave an example of the character "rounded forehead," considered by Frayer et al. (1993) to be a character linking north Asian *Homo erectus* to populations of modern humans in the same area. In reexamining this feature, Lieberman (1995) argued that because the feature is developmentally nonhomologous in the two populations, it is not a valid shared feature. Therefore it does not represent homoplasy in the recent origin model for modern humans and does not conflict with that hypothesis. Lieberman (1995) went on to discuss numerous other characters from the same point of view: for example,

shape of the occipital bone, lambdoidal flattening, the shape and slope of the frontal bone, facial prognathism, the shape of the malar (cheek) region, a ridge along zygomaticomaxillary suture, location of minimum frontal breadth, etc. Most of the traits Lieberman (1995) questioned had been used to support regional continuity between a population of *Homo erectus* or archaic *H. sapiens* and a population of modern humans in the same region.

Lieberman's analysis is very illustrative of the effects of character definition. By subdividing several of the traits used by some researchers to support a hypothesis of multiregional evolution of modern humans, he removed some of the evidence against a single origins model. In this case, homoplasy in certain traits inspired more detailed resolution of character states.

The importance of homoplasy in studies of modern human origins is not limited to character definition, as illustrated in some debates between Tattersall (1994, 1996, 1997) and Wolpoff (1994, 1997). Both authors at times use the principle of parsimony (informally) to justify a particular hypothesis of human origins, but in other cases they adopt the view that because homoplasy should be expected in closely related groups, certain hypotheses of homoplasy in their preferred phylogenetic trees should not be used as evidence against them. In other words, both favor a phylogeny that seems parsimonious in part because they are comfortable with the explanation for the homoplasy.

For example, Wolpoff (1994) criticized Tattersall's (1994) view that Neandertals and humans are different species and have distinct evolutionary trajectories because several similarities between Neandertals and humans would be forced to evolve in parallel. Tattersall (1996) retorted with statements that "Neanderthal-like" characters should be expected in some modern human populations, like the early humans from Europe, because Neandertals and humans are closely related and homoplasy among their populations is likely to be common. Therefore homoplasy is a weak argument against a recent origins of humans, who then replaced Neandertals in Europe.

Wolpoff (1997) later reversed his position on homoplasy, deciding that it could be used to support a multiregional argument for human evolution. His view was that homoplasy is so probable in closely related organisms that cladistic definitions of modern humans (tending to exclude Neandertals) cannot be trusted. Tattersall (1997), despite having argued previously for extensive homoplasy in closely related taxa, still favored the use of cladistic methods precisely because they reveal homoplasy.

Neither position is entirely convincing based only on discussions of the probability of homoplastic evolution, especially lacking a formal analysis, but the goal of this review is not to favor one phylogeny of the genus *Homo* over another. Instead, this example illustrates the view (sometimes implicit) that debates of phylogenetic hypotheses can be focused more or less rigorously on the plausibility of scenarios of homoplasy as much as they can be focused on analyses of parsimony.

SUMMARY AND CONCLUSIONS

Homoplasy is a conspicuous issue in primate systematics and phylogeny and has been for as long as people have studied human evolution. In the past, homoplasy, in the form of parallel evolution, was often considered the dominant theme in primate evolution. Today, it receives blame for difficulties in phylogenetic analysis but draws attention in the study of adaptation. In this review, we have emphasized several points.

First, not all, or even most, homoplasy is methodological error. There are many widely accepted biological processes in genetics, development, and biomechanics that should, and do give rise to detailed morphological similarity in disparate lineages. Without doubt, improved methodology related to both character definition and phylogenetic analysis will serve to correct some cases of apparent homoplasy. But a consistent application of more rigorous character definition will probably also reveal that some important synapomorphies are different in morphological detail or developmental or genetic basis. Better methodology will lead to an improved understanding of homoplasy, but *not* elimination of homoplasy. In fact, renewed attention

to homoplasy is probably a reflection of methodological sophistication and diversification of recent phylogenetic studies.

Recognizing and defining homoplasy is not always an easy task. In many respects, the identification of homoplasy is bound up with the identification of homology in the same organisms. In these definitions, there is a difference between pattern, or cladistic, definitions of homoplasy, and process, or evolutionary, definitions of homoplasy. A pattern definition, based ultimately on incongruence among characters (Patterson, 1982), is the most clear-cut method, but this approach is not satisfying because of its reliance on the parsimony criterion, and because it largely avoids interesting questions about process in morphological transformations. In any case, different definitions of homology and homoplasy are not mutually exclusive, and researchers are likely to choose an approach based on their particular research interest.

A promising trend in the study of form is to separate different levels of analysis (Bock and Cardew, 1999, and references therein). Homoplastic similarity at one level, such as adult phenotype, may coexist with homologous similarity at another level, such as development. This is the reason why many process-based definitions of homology are inconsistent with phylogenetic definitions. At the same time, the study of morphology at different levels of analysis is certain to provide a greater understanding of why homoplasy occurs.

Biological factors in homoplasy all develop out of the interplay of constraint (or potential) and natural selection. Our principal conclusion is that large gaps exist in the knowledge of how to compare character-based phylogenetic hypotheses, or just character distributions, to various evolutionary constraints in an explicit way. There is a difference in invoking constraint, such as development or allometry, to explain an observed pattern and tying it into the pattern directly.

Also, although many feel that some types of features (e.g., behavioral versus morphological) or some anatomical regions (e.g., teeth versus postcrania) are more prone to homoplasy than others, there is little solid

evidence to support such opinions. Similarly, while there is some theoretical basis to expect "adaptive," or strongly epigenetic, traits to be homoplastic, these expectations are largely untested. Our expectation is that the answers to these questions will turn out to be group specific, but empirical data is needed to address them in any event.

In many cases, it is not just new data that are required to understand homoplasy, but instead a greater synthesis of existing ideas and data sets. At a practical level, the combination of multiple sets of character data is useful for elucidating homoplasy (Yoder, 1994; Begun et al., 1997; Horovitz and Meyer, 1997; Ross et al., 1998). Furthermore, the extent to which biogeographic patterns, temporal distributions of taxa, and functional morphology can be used to inform phylogenies is a question of great current interest. Many feel that some kind of integration is required between morphological data and these other sources of evidence for evolutionary process, but an agreed-upon framework is lacking. Without that, the most interesting cases of homoplasy may remain conjectural.

Finally, we return to the status of homoplasy as troubling error to those interested in relationships, but golden opportunity to those interested in adaptation and evolution. The irony is that, in the current paradigm, knowledge of relationships is required by many researchers to study phenomena such as adaptation. Homoplasy hinders the task of obtaining that knowledge, but once relationships are known, homoplastic traits are often more easily explained than are their homologous counterparts. Patterns of homoplasy will therefore remain a preeminent source of information on how and why morphological change occurs, and a testing ground for models of biological process.

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